THE COMPARATIVE BIOLOGY OF *GLOBODERA ROSTOCHIENSIS* (WOLLENWEBER) AND *GLOBODERA PALLIDA* (STONE) (NEMATODA, HETERODERIDAE) IN THE SOUTH ISLAND OF NEW ZEALAND.

by

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ABSTRACT

An investigation into the biology of the potato cyst nematodes (PCN) Globodera rostochiensis (Ro) and G. pallida (Pa) was undertaken in the South Island of New Zealand. The study followed two basic pathways. (1) An examination of their ecology in order to identify factors which influenced their population biology and effect on the potato host. (2) A comparative study of the two species in the same geographical area where they were subjected to the same environmental factors. The two species were studied in isolation and in mixed cultures.

Potato cyst nematodes establish well in the South Island and multiply quickly under repeated annual cropping of the host. In replicated field microplots with low pre-plant densities a maximum multiplication rate of about 90x was observed. A mean maximum density of 300 eggs/ml of soil was measured and an equilibrium density of about 150 eggs/ml was achieved with continuous cropping.

Significant yield loss of host crop occurred at a pre-plant density of 15-20 eggs/ml of soil and the percentage crop loss increased at higher egg densities until maximum loss of 95% was obtained. No difference in the pathogenicity of the two species was detected.

Nematodes in early cropping ground at Outram had a much lower multiplication rate which varied through the season. Early harvesting of crops could reduce the multiplication rate substantially. If the crop was allowed to mature, multiplication rate rose by up to six times. The cyst population produced from early harvested crops could be divided into three components, (i) cysts produced early that fell off the roots at harvest and matured in the soil, (ii) cysts produced later that were still imbedded in roots as immature females at the time of harvest and developed to maturity on the moribund root and (iii) residual eggs which occurred within the cysts of the initial inoculum. Early maturing cysts made the greatest contribution to the inoculum potential for the following crops whereas residual eggs made the least. The presence of selfset potato tubers had differing influences on the three inoculum components.

Life tables were constructed for both species at three locations (soil types) and for two planting dates (soil temperature differences). Larvae within the cyst (life style A) had low mortality but once hatched and free in the soil (life style B) mortality increased. Soil temperature affected the level of mortality. Once established in root tissues (life cycle C) mortality decreased but rose sightly when adult females matured (life style D) and protruded into the soil. Soil

temperature and host vigour influenced the fecundity of developing females.

Comparisons of the two species in the same environment showed that Ro hatched earlier, and suffered less mortality and had a shorter duration than Pa in life style B. Once inside the root tissue (life style C) mortality of Ro was often greater than in Pa. Life styles C and D were also of shorter duration in Ro than Pa under most conditions.

When mixtures of the two species were kept together on the same host Ro was competitively superior and was proportionately more dominant in the next generation. This was observed over a range of Ro:Pa ratios. Reduction in overall nematode density appeared to improve the relative success of Pa. At very low proportions Pa is able to maintain its position and an equilibrium between the two species is established.

Spontaneous hatching (the major component of population attrition) in the absence of host stimulation occurred in both species and followed an exponential decline curve over time. Soil type influenced the attrition rates which were highest in Canterbury silts. Attrition rates differed significantly between species and were higher in Ro. Cyst size had little effect on the attrition rate. Reduction in egg numbers observed with time was largely a result of active egg hatching rather than within cyst mortality.

This study supplied the basic biological information on potato cyst nematode in the South Island of New Zealand, and when combined with the results of chemical control experiments and advances in the breeding of resistant potato cultivars has produced a largely successful control and management program for this pest.

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CHAPTER 1

INTRODUCTION

Globodera species are among the most highly specialised and successful plant parasitic nematodes. Six species are known to parasitize solanaceous plants such as potatoes and tomatoes. They belong to the family Heteroderidae and were placed in the genus Globodera by Mulvey and Stone (1976). Two species, Globodera rostochiensis (Wollenweber, 1923) and Globodera pallida (Stone, 1972), are known collectively as potato cyst nematodes (PCN). Both species occur in most potato growing areas, but before 1972 G. pallida went unrecognised or was considered a pathotype of G. rostochiensis. They are believed to have co-evolved with the potato in the Andean region of Peru and Bolivia (Evans et al., 1975) and they now occur along with their hosts throughout much of the world. In many countries potato cyst nematodes depress the yield of potato crops to an uneconomic level.

Control is difficult because this pest has a well developed host/parasite relationship which ensures good multiplication under a wide range of climatic conditions. The development of a large number of eggs in a persistent cyst stage at the end of the life cycle also ensures a high level of survival between host crops. In a commercial situation these small cysts are difficult to see and can be readily shifted with soil adhering to produce and to farm machinery.

The existence of two similar species, and at least eight genetically different pathotypes which are characterised by differences in host range has hindered understanding and successful control of this group of nematodes.

Increased use of G. rostochiensis resistant cultivars of potatoes revealed the existence of isolated pockets of "resistance breaking strains" (Dunnett, 1957) or pathotypes of potato cyst nematode. Many observations on the characteristics of these pathotypes have been reported. Guile (1966, 1967, 1970) recorded that the immature cyst of G. rostochiensis pathotype A changed to a golden colour shortly after rupturing the epidermis of the potato root, but that the cyst of pathotype E, of the same species (sensu latu), remained white for an extended period after its appearance on the root surface. Evans and Webley (1970) described differences in larval morphology and in the shape of the stylet knobs, and in the same year Jones et al. (1970) postulated that two species might be present. Trudgill et al. (1970) noted differences between the adult male of G. rostochiensis and the probable

undescribed species. Using electrophoresis, Trudgill and Carpenter (1971) subsequently demonstrated differences in protein bands from macerated immature golden and white females. Green (1971) recognised differences in vulval patterns of females of the two populations and soon after Stone (1972) reported a consistent difference in the lip structure of second stage larvae from each population. Parrott (1972), and Franco and Evans (1978) demonstrated that the two forms would not interbreed. A second species was finally described by Stone (1972) as Heterodera pallida.

Interbreeding experiments continued with the work of Kort and Jaspers (1973) who questioned the findings of Parrott (1972) as they found the two species could interbreed and produce hybrids. Using a new culturing technique Mugniery (1979) showed that both species would interbreed but that the resultant progeny were infertile. In this way G. pallida was firmly established as a distinct species.

Several pathotypes of G. rostochiensis and G. pallida are now recognised in all countries harbouring the pest, but the nomenclature used to describe them has not been consistent and it has been difficult to determine which pathotypes were common to different regions. Kort et al. (1977) clarified the situation by proposing an international scheme for classifying pathotypes of G. rostochiensis and G. pallida (Table 1.1). This has been adopted internationally and the nomenclature is followed in this study.

TABLE 1.1

International nomenclature for describing pathotypes of *G. rostochiensis* and *G. pallida*. (According to Kort *et al.* (1977)).

Differentiating plant	Plant resistance code	Pathotype							
		Ro_1	Ro_2	Ro_3	Ro_4	Ro_5	Pa_1	Pa_2	Pa_3
S. tuberosum ssp. *tuberosum*	-	+	+	+	+	+	+	+	+
S. tuberosum ssp. *andigena* CPC 1673	$Ro_{1,4}$	-	+	+	-	+	+	+	+
S. kurtzianum hybrid 60.21.19	$Ro_{1,2}$	-	-	+	+	+	+	+	+
S. vernei hybrid 58.1642/4	$Ro_{1,2,3}$	-	-	-	+	+	+	+	+
S. vernei hybrid 62.33.3	$Ro_{1,2,3,4}$ $Pa_{1,2}$	-	-	-	-	+	+	+	+
S. vernei hybrid 65.346/19	$Ro_{1,2,3,4,5}$	-	-	-	-	-	+	+	+
S. multidissectum hybrid P55/7	Pa_1	+	+	+	+	+	-	+	+
S. vernei 69.1377/94	$Ro_{1,2,3,4,5}$ $Pa_{1,2,3}$	-	-	-	-	-	-	-	-

Ro = *G. rostochiensis*

Pa = *G. pallida*

\+ = Species and pathotype will reproduce on this clone.

\- = Species and pathotype will not reproduce on this clone.

1.1 DISTRIBUTION OF POTATO CYST NEMATODES IN NEW ZEALAND

Dale (1972) reported the discovery of potato cyst nematode in New Zealand at Pukekohe, an early potato growing district. Plant inspectors of the Ministry of Agriculture and Fisheries (MAF) were seconded from all districts in New Zealand to survey Pukekohe potato crops in 1973 and in the following seasons they inspected crops elsewhere.

In 1975, Marshlands and Cranford Street, adjacent to Christchurch, were found to be infested, and in 1976 nematodes were found at Outram and Port Chalmers near Dunedin. Isolated infestations were found in the seed producing areas of Waddington and Halkett (Figure 1.1) in 1975, and in home gardens in Christchurch, Oamaru, Palmerston, Alexandra and Invercargill. Subsequently, surveys have been carried out annually in all potato producing areas of New Zealand but new infestations have been confined to the previously known areas of infestation.

Although the sites of nematode infestation are widely distributed, only three commercial potato producing areas are known to be infested. They are Pukekohe (582 ha), Christchurch (1018 ha) and Dunedin (281 ha) (Davie, Hubbard and Harding pers. comm.) which together represent 2.2% of the total cumulative potato area (82,920 ha) registered during the last 10 years.

1.2 DISTRIBUTION OF SPECIES AND PATHOTYPES IN NEW ZEALAND

Wouts (1976) verified that both species were present in New Zealand and the major known populations have been pathotyped by Foot (pers.comm.) and myself. The known distributions of these pathotypes are shown in Figure 1.1. Further details of cropping patterns and pathotype occurrence are given in Table 1.2. For management purposes all infested fields are considered to be separate populations and are assigned a coding by MAF personnel to identify the district and fields infested. The species have been found both as pure and mixed populations and their distributions have no obvious geographical pattern.

FIGURE 1.1

Outline map of New Zealand showing known distribution of potato cyst nematode.

Place names in upper case indicate infestations in areas of commercial potato production, place names in lower case indicate infestations in domestic gardens. Underlined names indicate major towns adjacent to infestations.

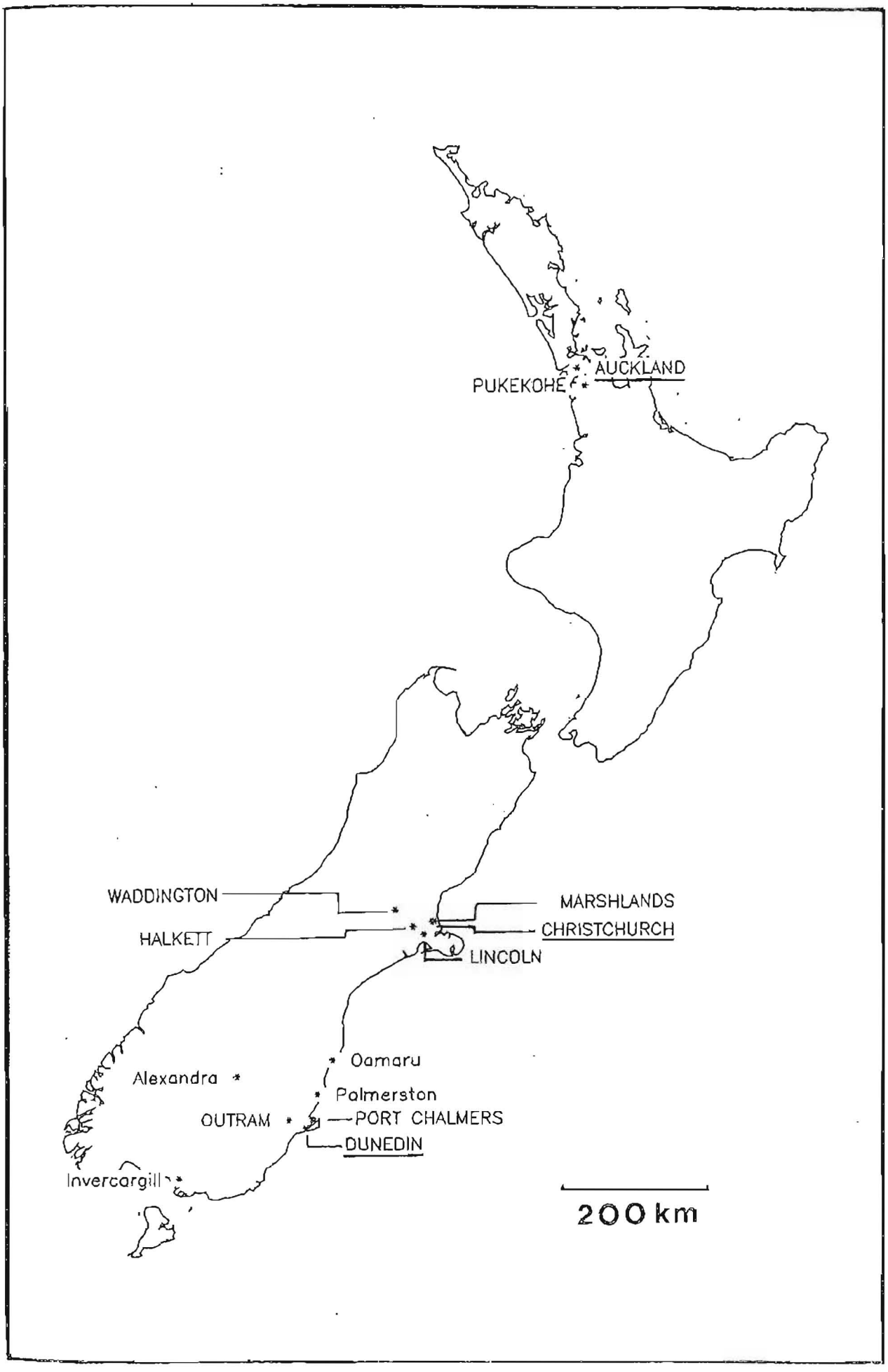

AUCKLAND
PUKEKOHE
WADDINGTON
HALKETT
MARSHLANDS
CHRISTCHURCH
LINCOLN
Oamaru
Alexandra
Palmerston
OUTRAM
PORT CHALMERS
DUNEDIN
Invercargill
200 km

TABLE 1.2

Species and cropping patterns associated with PCN infestation in New Zealand. Order of predominance of pathotype shown where known.

Location	Cropping pattern	Pathotypes present in order of predominance
Pukekohe	Early crop	Pa_2 Pa_3 Ro_1
Christchurch	Early and main crop	Ro_4 Pa_3 Ro_1
Waddington	Seed crop	unknown
Halkett	Seed crop	unknown
Oamaru	Home garden	Ro
Palmerston	Home garden	Pa
Outram	Early crop	Ro_1
Port Chalmers	Early and main crop, home garden	Ro_4 Pa
Invercargill	Home garden	Pa
Alexandra	Home garden	Ro

1.3 POTATO CULTURE IN THE SOUTH ISLAND OF NEW ZEALAND

Potato growing is widespread in the South Island where the principal cultivar is Ilam Hardy. Ilam Hardy is planted in spring (September-November) and in areas close to urban centres some crops may be harvested in December to meet the Christmas demand for new potatoes. However, in all districts the bulk of the crop is left to mature and is not lifted until autumn (April-May). Crop rotation is practised on most large holdings, but on the smaller intensively farmed horticultural units it is not uncommon for successive crops of potatoes to be planted on the same ground.

The market gardens of Outram and Port Chalmers have a unique cultural pattern. There, early potatoes are the principal crop and specially acclimatised seed potatoes are sprouted (chitted) before planting in mid-winter (July-August). These potatoes mature rapidly and are harvested at the end of November when they command a premium price. Following this crop the ground is cleared, cultivated and replanted in oats, a green crop which grows until May when it is dug in during ground preparation for potato planting in the following July-August. Other main crop potatoes grown in the Otago district follow the normal spring planting pattern.

1.4 RESEARCH RATIONALE

With the discovery of potato cyst nematode at Pukekohe, the Ministry of Agriculture and Fisheries devised and implemented a policy designed to contain and control the pest (The potato cyst nematode regulations 1974, Government Printer 1974/220. Ministry of Agriculture and Fisheries 1975). This policy is still in force and all aspects of research are subject to the strict quarantine requirements set out in the policy. Initially MAF, policy was based on overseas information. To provide more substantial data Nematology Section of the Department of Scientific and Industrial Research (DSIR) commenced research on the control and biology of potato cyst nematode in New Zealand, and Crop Research Division of the DSIR initiated a resistance breeding program for both *G. rostochiensis* and *G. pallida*.

Nematological research began at Pukekohe. It concentrated on *G. pallida* which, at the time, was the only species known in New Zealand. However, after potato cyst nematode was discovered in the South Island (1976) research was regionalised and I was made responsible for the South Island program.

The presence of infestations of both species in the South Island, a range of soil types, diverse environments and different cropping

patterns confused interpretation of biological events and implementation of control procedures. This was further confounded by the appearance of mixed populations at many of the infestation foci.

Clearly, before a long term strategy could be devised for control of the pest in the South Island, essential ecological information was required. Different cropping practices, climate, soils and population composition largely precluded direct application of North Island experience to the South Island situation.

This study was designed to provide an understanding of the biology of the two Globodera species in South Island infestations and to provide the basic information on which to build sound policy.

The objectives were:-

1. To monitor the dynamics of a range of populations and to explain rates of increase and decline.
2. To interpret developmental biology and identify key components in survival/mortality events.
3. To investigate possible interactions between the species in mixed populations.
4. To define host responses to levels of parasitism.

This thesis is presented in the following form.

A description of research sites, operation of quarantine at these sites and the management of host and inoculum is given in Chapter 2. In addition a description is given of specific experimental techniques used for inoculating, growing, recovering and recording both cyst numbers in the soil and developing larvae in the roots.

Host responses to different levels of potato cyst nematode in a simulated field situation are given in Chapter 3 where the dynamics of each species and the effects they have on the host were examined. The life history of a G. rostochiensis population at Outram was studied and the influence of different inoculum sources on the population dynamics were examined and are presented in Chapter 4.

Chapter 5 presents the developmental biology of both species in different environments and soil types. Key factors in the mortality of each life history are discussed and species differences highlighted.

Interactions between mixtures of both species on the same host are investigated in Chapter 6 and the probability of single species dominance in a field population is discussed.

In Chapter 7 changes in egg numbers and the status of the eggs within dormant cysts are examined and the influence of species, soil type

and cyst size are examined in relation to the rate of natural population decline.

The entire study is reviewed in Chapter 8 and the basic biology of PCN in the South Island is discussed and considered in a broader context.

CHAPTER 2

GENERAL

2.1 RESEARCH SITES

As required by the potato cyst nematode Regulations MAF 1974, research was carried out under strict quarantine conditions. An enclosed compound known as "S4" with an area of 0.5 ha and divided into three sub units is used by different research groups. The groups consist of DSIR nematologists and plant breeders, and MAF plant health and diagnostic staff who process all survey and diagnostic material. The research area used by the nematology group (Figure 2.1) is divided into three isolated plots, one for G. rostochiensis infestations, one for G. pallida infestations and another for mixed species studies. S4 experimental area is situated on the free draining soils of the Waimakariri fan which are composed mainly of stony greywacke alluvium and in places a thin layer of loess (Cox, 1978) (Figure 2.1). A profile description of S4 soil types is given in Appendix I.

In addition to S4, research has been carried out at Cranford St. which is located on the highly organic peats north of urban Christchurch. Soils of this area developed behind coastal sand dunes and when drained are highly productive. They have supported horticulture since the 1870's (Raeside and Rennie, 1974). Research plantings at Cranford St. (Figure 2.2) were made in fibrous brown partially decomposed peat which had been broken down by extensive cultivation (Figure 2.2). The area is drained by extensive tile and open drains and does not puddle in winter. Occasional flooding of the whole area occurs, however. A profile description is given in Appendix II.

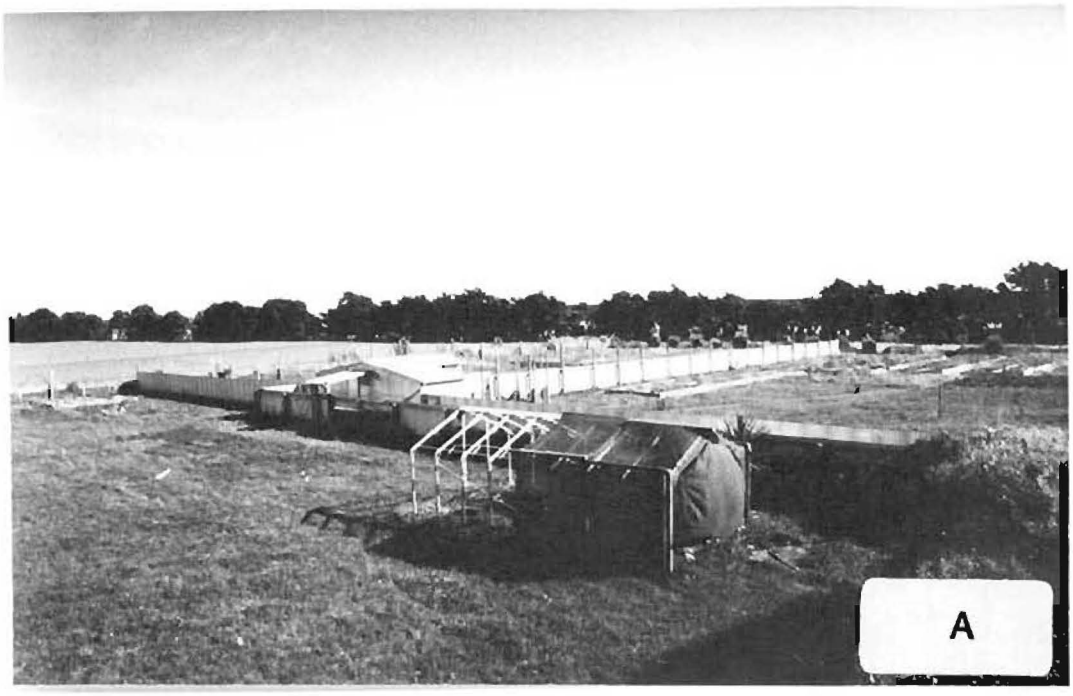
Outram, 11 km from Dunedin is situated on the flood plain of the Taieri river. The Clutha silt loams of Outram (Figure 2.3) are confined to a small geographic area derived from flood plains produced by the Taieri River. Profiles vary considerably because of the fluvial origins of the soil, but the principal parent material is schist. A little basic volcanic alluvium also occurs. This soil heats up quickly and has good drainage. The research area at Outram is sited on a gently sloping bank with a north facing aspect. Detailed soil profiles are included in Appendix III.

To ensure that the infestations did not spread from the experimental areas, all areas were fenced with wind-break cloth and topped with barbed wire. Access was restricted to DSIR staff. Cranford St. which is prone to flooding, has a corrugated iron footing embedded around the fence line to deflect flood waters (Figure 2.2).

FIGURE 2.1

General view of nematology research area.

Soil profile of S4 showing soil layers (changes in profile marked by arrows) and underlying shingle and stones.


A


B
200
mm

FIGURE 2.2

General view of Cranford Street research area showing wind-break cloth and corrugated iron footing embedded around the fence line.

Soil profile of Cranford St., showing upper layer of finely cultivated peat sitting on top of fibrous partially decomposed peat, clay and tree roots. Changes in profile marked by arrows.

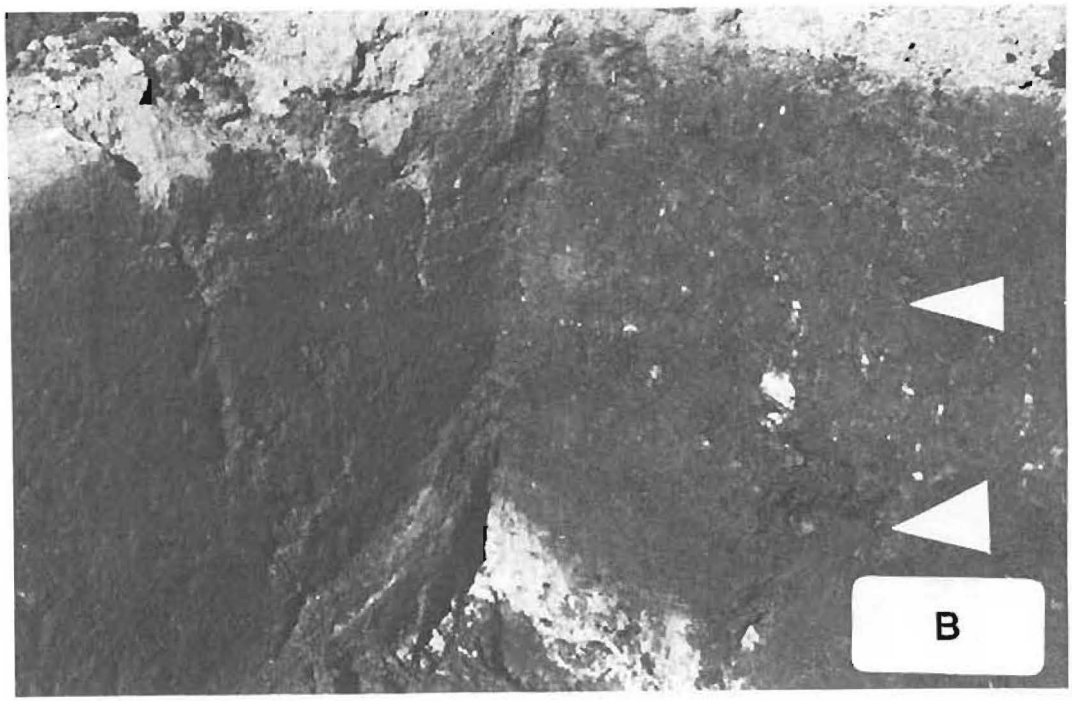


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FIGURE 2.3

General view of the Outram research area showing wind-break cloth fence and tin microplots.

Soil profile of Outram; upper layer modified by the inclusion of organic material from cropping; lower levels largely silts and fluvial sands. Changes in soil profile marked by arrows.

200
mm

2.2 OPERATION OF QUARANTINE

Access to S4 is restricted to authorized staff who are trained in quarantine procedures. The unit is defined by a 1.8 m high barbed wire fence with a 1 m wind-break cloth battened at the bottom and is protected from the prevailing north-west winds by a shelter belt of conifers. All cultivation and harvesting is carried out with equipment permanently located in the compound.

Waste material is either burnt or dumped in deep pits located within the unit. Potato tubers are decontaminated (Figure 2.4) with a 1% solution of sodium hypochlorite (Wood and Foot, 1977a) prior to removal from the unit and are dumped in a local pit and buried. All unprocessed soil and cysts are devitalised by heat in an oven at 100°C for 24h before being dumped into the pits. All concrete work areas are graded to ensure that waste water flows off into settling tanks and enclosed soak pits. All areas are washed down thoroughly after use.

On the subsidiary research areas at Cranford St. (Figure 2.2) and Outram (Figure 2.3) plant and soil samples collected are sealed in multiwall paper bags and removed to S4 for processing and disposal.

2.3 INOCULUM

With one exception all nematodes used in experiments were pure populations of *G. rostochiensis* (Ro_4) and *G. pallida* (Pa_3). At Outram the resident pathotype was *G. rostochiensis* (Ro_1).

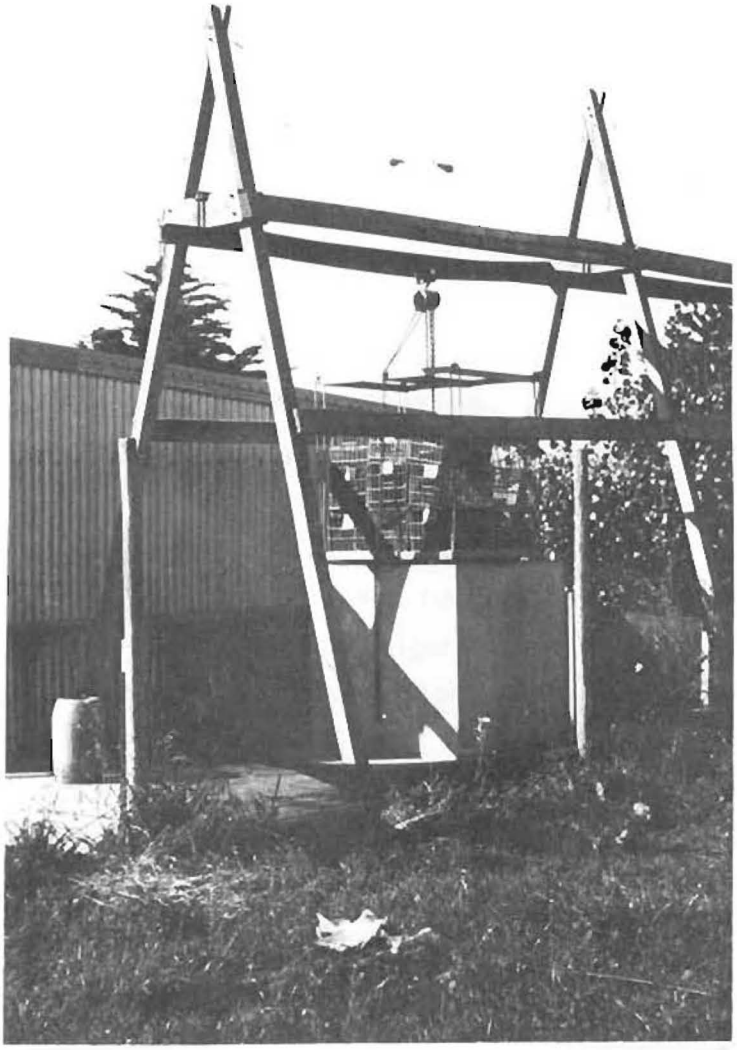
Original populations were obtained from natural field populations in Canterbury and Outram. Pathotype purity and identity was confirmed by screening over the range of genetic differentials established by Kort *et al.* (1977) (Table 1.1).

Inoculum was multiplied on an Iram Hardy potato under field conditions. Cysts used in the experiments were produced as single generation populations, all of the same age and uncontaminated by parental cysts. All cysts used were produced the season prior to their use. After the host plant and tubers had been removed, cysts and soil were placed with potting mix in a terylene bag and buried in a field plot at S4 until needed. All cysts stored this way were used within nine months.

FIGURE 2.4

Equipment used to decontaminate potato tubers prior to removal from S4 compound.

Infested tubers are loaded into baskets in lifting frame and lowered into decontamination tank for two hours. After this time the baskets are lifted out, and the tubers washed down and moved out of the compound on the overhead rail.



2.4 HOST

Government certified (Group one) Iiam Hardy potato seed was obtained from the same grower's line and used in all experiments. This cultivar is susceptible to both species of nematode and is the dominant cultivar grown in New Zealand, comprising 46% of the total potato plantings. Tubers were hand selected on the basis of size (50-100 g) and freedom of surface pathogens.

2.5 FIELD EXPERIMENTS

Where possible, experiments were carried out in the field. This was achieved either by using terylene bags which contained an individual plant rhizosphere in a field environment or by using tin microplots.

2.5.1 Single host units

Terylene bags similar to those used by Foot (1978) were used to allow individual plants to be exposed to a predetermined nematode density and also to allow subsequent intact retrieval of an entire plant root system and its associated nematode population. This ensured that sampling of nematode progeny was efficient as none of the soil was lost during harvest.

Terylene bags were sewn double walled, but differed from those used by Foot (1978b) in that they were in the form of a sewn tube of 125 micrometre single thickness terylene mesh (Figure 2.5A) which was pushed inside itself "hose on hose" when in use to form a double skinned bag with a soil capacity of 2.0-2.5 litres (Figure 2.5B). This modification facilitated bag manufacture and the removal of both the soil and the growing plant, especially after vigorous root development. Although some root hairs grew through the double skin, the majority of the roots were effectively contained inside the bag.

2.5.2 Field Microplots

Field microplots were used to determine multiplication rates and equilibrium densities under field conditions. The 20 plants used in each plot were considered to be sufficient for analysis of yield responses to different nematode concentrations.

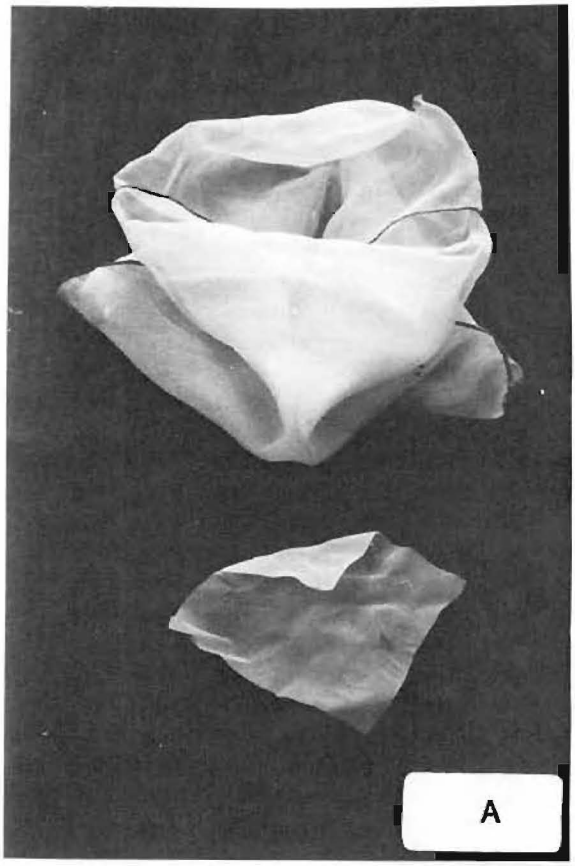
Microplot units (Figure 2.6) were constructed of 0.95 mm galvanised flat iron. Each unit was folded to size and spot welded or pop riveted together on site. Walls were 600 mm deep and were placed in a trench to half this depth. The trench was excavated with a self propelled chain trencher which minimised disruption of the soil profile.

FIGURE 2.5

Terylene bags with "hose on hose" double wall construction and squares of terylene used as sachets.

Terylene bags with a single potato plant (referred to in text as a single host unit) and inoculum sachets combining cysts and 5 ml of soil.

Potato plants growing in terylene bags during life table experiments. (Scale: one division = 20 mm).



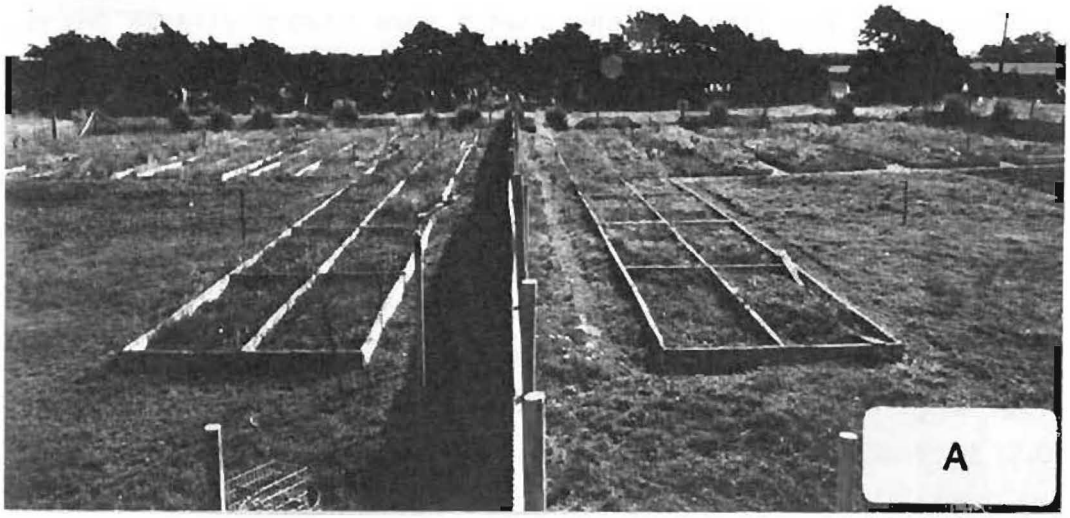

C

FIGURE 2.6

Tin microplots which were formed from galvanised flat iron embedded in the ground contained both infested and clean plots of soil. These plots were used to determine host response to attack by both species of potato cyst nematode.

A. A general view of the microplot area at S4 showing the identical arrangement of the plots used for Ro and Pa. (Pa on left, Ro on right).

B. Close up view of single plot showing nematode damage and an adjacent uninfested control plot.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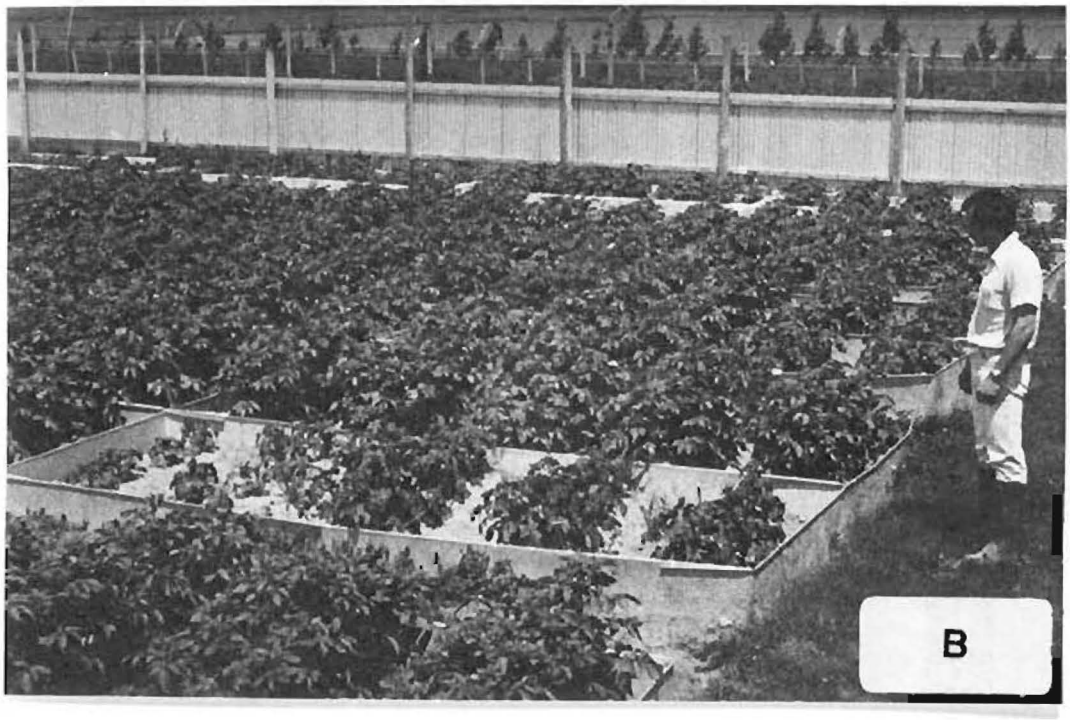
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Each unit was made up of eight equal sized plots 9 x 1.4 m. This area was calculated from normal commercial potato plant spacings, i.e. 760 mm between rows and 300 mm between tubers. Four tubers were planted per row so as to minimise container edge effects which gave a total of 20 tubers per plot.

In each unit, four of the eight plots selected from random number tables were inoculated with nematodes at first planting. The nematodes were dispersed equally around each tuber, and the soil was then moulded up. The remaining four plots, were used as non-inoculated controls.

Plots were cultivated by hand forking and with a small portable garden rotary hoe. Seed potatoes were planted and moulded by hand.

Selected 50-100 g seed tubers (Government certified Ilam Hardy) were planted in all plots. Weed control was obtained with Sencor (Bayer Metribuzin) at the equivalent of 0.50 kg/ha applied as a post emergence herbicide. Solanaceous weeds such as hairy nightshade (Solanum sarrachoides) that were not killed by Sencor were controlled with spot applications of Basogran (BASF Bentazone) at the equivalent of 2.0 litres/ha. Soil fertility was assured by applying potato fertiliser (N_4. P_5. K_0. S_{11}.) at the equivalent rate of 625 kg/ha at the time of planting. Fertiliser was incorporated into each row. Water was applied with a portable agricultural overhead sprinkler (Rainbird Harvins with a 5 mm jet) and the equivalent of 25 mm of rain was applied at a time. The frequency of application was determined subjectively, but ensured that plants were never water stressed.

If late blight (Phytophthora infestans) conditions of high humidity and temperature were imminent, a blanket application of Ridomil (Shell Metalaxyl) at an equivalent rate of 1.0 kg/ha was applied to all plants in the research area. Blight conditions are rare in Canterbury, and Ridomil resistance was not encountered.

The crop was harvested after the plants had died down and the root system had decayed.

2.6 INOCULATION

2.6.1 Sachets

Inoculum was dispensed in sachets (Figure 2.5 A&B) which were constructed of 125 micrometre mesh terylene cloth. The terylene was cut into 150 x 150 mm squares and cysts plus 5 ml of graded 250-600 micrometre soil were placed on them. The sachets were closed with a twisted wire closure. Eight sachets were used to distribute the inoculum through the soil within each bag. The inclusion of 5-10 ml of soil in sachets was considered to be essential as it appeared to maintain a

continuity of soil moisture which allowed the cyst hatching factor to stimulate hatching (Jones and Winslow, 1953). On one occasion when only cysts were included in the sachets the host plants did not become infected.

Sachets were placed in the bags at the same level as the tuber and equidistant between it and the side walls of the bag. Exact placement is probably not important as Foot (1978b) found it had little effect on the final multiplication of the nematodes. At the end of plant growth sachets were retrieved and hatching success was determined.

2.6.2 Egg suspensions

When the two species were at low egg densities during the interaction experiments, inoculation with free eggs (i.e. released from the cysts) was required. Cysts were crushed gently in a tissue grinder and shaken in a small volume of water to disperse the eggs. The resulting egg suspension was adjusted with distilled water to produce the required number of eggs/ml of water.

A suspension was injected with a large bore syringe into the soil around an actively growing plant and watered in.

2.7 RECOVERY OF CYSTS FROM SOIL

2.7.1 Mature cysts

To recover cysts, the infested soil was air dried (15-20°C) and cysts were concentrated by washing through a modified Fenwick can (Figure 2.7A) as described by Wood and Foot (1977a). The elutriated material was collected in a pair of Endecott sieves of mesh size 850 micrometre and 250 micrometre, respectively. The larger sieve removed unwanted rubbish and the smaller retained the cysts; anything smaller than 250 micrometres was discarded.

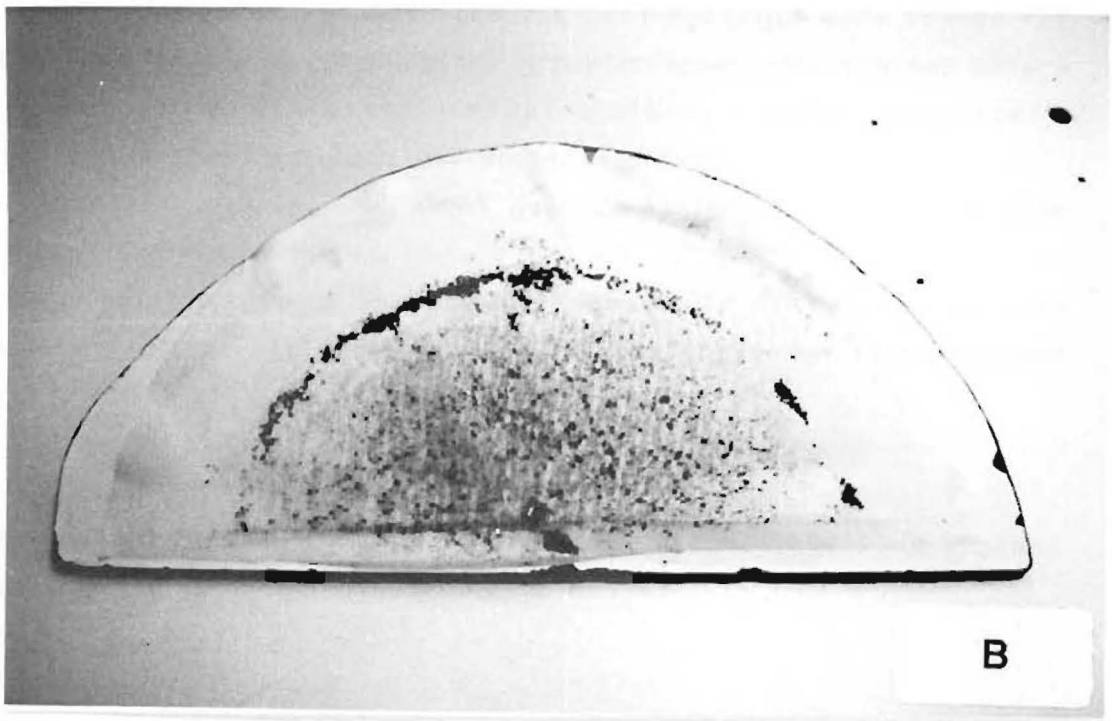
Cysts were washed onto a 100 mm diameter filter paper disc and the water was drained away. If large quantities of organic matter were present in the funnel, a second wash with 95% ethanol was carried out. This caused the cysts to float clear of the debris and accumulate in a ring around the top of the filter paper. The drained cysts and filter paper were spread out on a semi-circular counting plate (Figure 2.7B) and examined with a stereoscopic microscope at 6-40 x magnification. Cysts were picked off the filter paper with forceps and stored in 25 ml brown glass bottles.

FIGURE 2.7

A. Modified Fenwick can used to separate dry cysts from a soil sample. The sieves separated the coarse debris from the cysts.

B. The cysts and fine debris were collected on a semi-circle of filter paper and counted under a stereoscopic microscope.


A


B

2.7.2 Immature white cysts

Immature cysts will not float after air-drying the soil and hand sorting a soil sample is labour intensive. To alleviate both problems, the immature cysts were extracted immediately after the sample had been collected. White cysts will remain suspended in a column of water for a short time and if the water is decanted rapidly the cyst will be carried over with the water. A simple system of agitation and decantation which took advantage of this cyst behaviour was developed and is detailed as follows.

A 100 ml soil sample was placed in a 710 micrometre mesh sieve with a 250 micrometre mesh sieve beneath. The sample was washed vigorously through the sieves and the material retained on the smaller sieve was collected. Coarse sediment and cysts retained by the 250 micrometre sieve were washed into a white sorting tray (300 x 300 x 75 mm) which was filled to a depth of 25 mm. The sediment and water were sluiced to and fro until most of the white cysts were suspended in the water. They were decanted onto a 250 micrometre sieve, the tray was refilled with water, and the process was repeated until no more white cysts were detected. The concentrated cyst sample was then washed into a Doncaster counting cell (Doncaster, 1962) for counting.

2.7.3 Cyst viability

Contents of all cysts were examined for viability using the vital stain New blue R, also known as Meldola's blue (Shepherd, 1962a). A 0.05% solution in water was used and the cyst contents were soaked for 48h. Dead eggs took on a purple/black granular appearance whereas mature live eggs and larvae exhibited minimal staining and were opalescent. Empty egg shells remained unstained and transparent.

This rapid staining technique gave consistent separation of live and dead eggs and empty shells.

The viability of eggs in immature cysts could not be assessed with this technique as the stain did not differentiate between live and dead eggs.

2.8 ASSESSMENT OF LARVAE IN ROOTS

To render larvae more visible in root tissue they were stained before extraction.

2.8.1 Staining

Standard Cotton Blue lactophenol (Southey, 1970) was used to stain nematodes in roots. Washed potato roots were cut into 10 mm sections and

dropped into boiling lactophenol containing 0.1% Cotton Blue for five minutes after which the roots were cooled and left to stand in clear lactophenol for 24h. The boiled roots and liquid were washed over a 150 micrometre sieve which retained roots and dislodged cysts which were transferred to clear lactophenol prior to examination. Material treated in this way did not deteriorate with extended storage.

2.8.2 Extraction

A 5 g root sample was macerated in an 'MSE' blender for 20 sec and particles smaller than 250 micrometres were sieved off and stored. Root particles larger than 250 micrometres were remacerated for an additional 20 sec and resieved. This process was continued for a total of 60 sec.

This stepwise maceration/sieving technique removed the larvae before they could be damaged by extended maceration. Marks and McKenna (1981) developed the extended maceration technique on whole samples but found that L_2 larvae were destroyed (Marks pers.comm.) The smaller than 250 micrometre fraction was diluted in 200 ml of water and stirred before a 25 ml subsample was removed and placed in a glass bottomed plankton counting chamber. Fifteen ml of 1% 'Calgon' (sodium hexametaphosphate) dispersant was added and the chamber was topped up with 25 ml of water. The fine plant tissue remained dispersed and slowly floated to the surface while the stained larvae sank to the bottom of the chamber. If the plant tissue in the sample aggregated before reaching the top of the column it was discarded and replaced by a smaller 12.5 ml sample. This procedure was necessary as the aggregated tissue trapped the smaller L_2 larvae. Recovery of larvae was shown to be as good as hand separation (Appendix IV) and an increased number of samples could be processed in a day. All nematodes present in a sample were counted using an inverted compound microscope (Figure 2.8) at 100x magnification. All larval stages were recognised and classified as second, third or fourth stage (Figure 5.2).

2.9 ANALYSIS OF DATA

All data collected were entered directly on computer punching sheets, stored on a floppy disc and transferred to main frame storage.

All analysis was performed on the DSIR main frame VAX computers and local work stations using statistical packages "Genstat" and "Minitab".

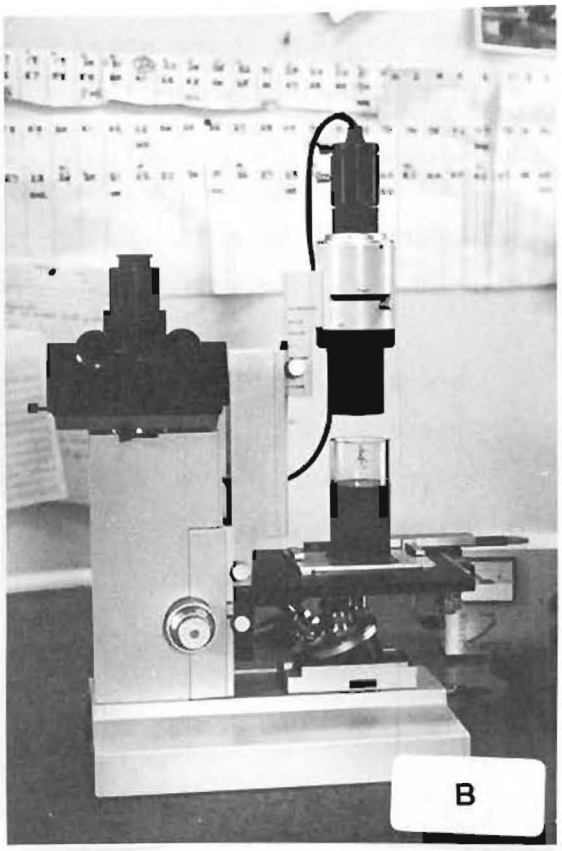
Significant differences (using Students t test) between sets of data at the 5% level are expressed in the text as ($P<0.05$). A non significant difference is indicated by ($P>0.05$). Log transformations of

FIGURE 2.8

A. Arrangement of stereoscopic microscope used to count cysts extracted from dry soil.

B. Glass bottomed settling chamber in position on an inverted microscope prior to counting the nematodes which have settled out from suspended plant tissue.


A


B

data are all to the $\log_{10}$.

The "Edit" package was used to manipulate the data files. The "PN graph" package produced the graphics which were plotted on a Hewlett-Packard x-y plotter.

2.10 SOIL TEMPERATURE AND MOISTURE DETERMINATION

Soil temperature

At all three sites a probe connected to a battery operated "Grant" paper-tape recorder was used to record the soil temperature continuously at a depth of 100 mm. These units ran for the duration of the study and the minimum and maximum daily temperatures were transcribed from the tapes and stored on a computer file. For the life table study (Chapter 5) daily means were calculated. In the attrition study (Chapter 7) weekly means were calculated so that seasonal differences between soil types could be examined.

Soil moisture

Soil moisture was recorded weekly for the duration of the study. Four, 250 ml soil moisture cans with lids were filled with soil from the top 100 mm at each study area.

The Outram sample was obtained by a farmer who sealed the tins and posted them to Lincoln. The tins plus soil were placed in a drying oven 90°C for 24h. Soil moisture was taken to be the loss of weight expressed as percent oven dry weight.

CHAPTER 3

POPULATION INCREASE AND CROP LOSS

3.1 INTRODUCTION

Understanding the relationship between nematode density and crop losses is fundamental to any program established to develop control and management strategies.

Although it is generally recognised that the relationship between nematode numbers and yield is primarily a function of pre-plant densities (Oostenbrink, 1966: Seinhorst, 1965, 1968, 1970, 1982; Jones, 1969; Seinhorst and den Ouden, 1971; Bumbulucz and Oydvin, 1976; Foot et al., 1980; Stelter et al., 1980) specific nematode responses such as multiplication rate, maximum density, equilibrium point and equilibrium density must also be determined to understand the dynamics of this relationship.

In the South Island of New Zealand this basic information was not available for either species of potato cyst nematode, and there was no information on the comparative responses of the two species in the same environment, a subject on which the available literature also appeared deficient.

To provide information on the dynamics of both nematode species and host response, separate field based "tin microplots" (Chapter 2.5.2) were established. Uninfested control plots were maintained to compare yield responses between infested and uninfested host plants. The experiments reported in this study ran for three years.

3.2 METHODS

3.2.1 Experimental design

Microplot methodology developed by Jones (1956) was used in this experiment as it simulated field conditions and normal plant growth and largely avoided the sampling problems associated with patchy nematode distributions.

The randomised block design of both infested and control plots produced a more rigorous statistical data base for both nematode and host responses. In this study four microplots for each species were initially inoculated initially with a range of nematode densities and a crop of potatoes was grown to establish the population in the soil.

Both Pa and Ro were established separately in identical microplots at similar initial densities (Table 3.1).

TABLE 3.1

Pre-plant densities (eggs/ml) for both Pa and Ro in original and revised microplot experiments.

Original experiment 1979 - 1981 (n=4)

	Plot number 1		2		3		4	
	mean	(+SE)	mean	(+SE)	mean	(+SE)	mean	(+SE)
Species								
Pa	3.4	(±0.46)	7.3	(±6.15)	13.1	(±2.05)	20.5	(± 6.67)
Ro	3.8	(±1.14)	8.6	(±7.56)	15.4	(±3.06)	81.8	(±27.7)

Revised experiment 1981 - 1982 (n=3)

	Plot number 1		2		3		4	
Species								
Pa	3.0	(±1.4)	10.0	(±2.6)	50.0	(±6.8)	100.0	(±24.2)
Ro	3.0	(±1.9)	10.0	(±3.4)	50.0	(±9.1)	100.0	(±31.6)

The rationale behind the use of a range of initial densities was to shorten the time needed to observe the changes in nematode numbers from the lowest detectable density to the highest sustainable density. It was considered that the time taken to follow a single population through the natural development of population densities was beyond the time scale of this thesis research.

The experiment began in 1979 and at the end of the 1980-81 season the yields of most infested plots were severely affected by the nematode. At the same time it was apparent that pre-plant densities between 10-100 eggs/ml of soil were not well represented and this showed up clearly in the curve relating pre-plant density and multiplication rate.

The original experiment was stopped except for one microplot set and the control plots of all other microplots were used to set up a new set of microplots in which required nematode densities were established. They were produced by shifting appropriate quantities of infested soil containing high density populations into non infested plots (Table 3.1).

Management of the original and modified microplot experiments has been outlined in Section 2.5.2.

3.2.2 Assessment of population density.

After each harvest the soil was raked level and thoroughly mixed with a small cultivator (Chapter 2.5.2). The mixed soil was raked and left until the following spring when it was recultivated, fertilised and the pre-plant density of nematodes determined.

From each replicate plot (including the controls) five soil samples were collected. Each sample was made up of ten, 100-150 ml soil samples collected with a garden trowel at equal spacings along the microplot length. Samples were bulked into a plastic bucket, mixed thoroughly and a 200 ml composite sample was removed. The remaining soil was thrown back onto the plot. This procedure was repeated at five equally spaced points across the plot. During the course of the experiment the post-harvest level of the preceding generation was used as the pre-plant value for the following crop. In this way any natural population attrition between crop harvest in autumn and replanting in the following spring was eliminated from the pre-plant density determination. Treatment of soil samples is detailed in Sections 2.7.1 and 2.7.3

3.2.3 Assessment of host yield.

After natural plant senescence, tubers were dug from each microplot and stored in a labelled multiwall paper bag. At the completion of harvest tubers from each microplot were graded for weight,

(> 100g table size; < 100g, seed size) and number. The raw data were stored on computer file. Mean plot weights and numbers for both sizes were calculated.

To eliminate year to year variation, all data are expressed as percentage loss relative to the controls of the relevant season.

3.3 RESULTS

3.3.1 Population dynamics

Changes in the density of viable eggs per ml of soil from year to year were recorded for both species in each microplot and are presented in Table 3.2.

TABLE 3.2

Egg density (eggs/ml) in four microplots for the two nematode species between 1979 and 1982 (n = 4).

	1	2	3	4
Year	mean (±SE)	mean (±SE)	mean (±SE)	mean (±SE)
		Pa		
1979	7.3(± 6.15)	3.4(± 0.46)	20.5(± 6.67)	13.1(± 2.05)
1980	134.7(±31.4)	297.7(±13.3)	329.5(±33.17)	229.7(±18.59)
1981	249.7(± 8.19)	236.0(±30.6)	253.0(±36.5)	215.0(±28.0)
1982	- -	- -	- -	97.7(±21.83)
		Ro		
1979	8.6(± 7.56)	3.8(± 1.14)	81.8(±27.7)	15.4(± 3.06)
1980	156.5(±96.8)	336.2(±30.1)	424.5(±53.2)	422.5(±65.9)
1981	224.0(±124.4)	220.0(±52.4)	281.7(±50.49)	298.0(±44.5)
1982	- -	133.3(± 8.57)	- -	- -
		Pa		
1981	3.0	10.0	50.0	100.0
1982	63.1(± 1.4)	100.3(± 2.6)	21.3(± 6.8)	116.6(±24.2)
		Ro		
1981	3.0	10.0	50.0	100.0
1982	110.0(± 1.9)	217.0(± 3.4)	229.2(± 9.1)	75.0(±31.6)

Figure 3.1 shows the relationship between pre-planting and post harvest population densities for both species in the microplots. There was an initial rapid increase in population density (eggs/ml) and most populations reached maximum density within one or two generations (Table 3.2). Mean maximum population density (Table 3.3) obtained by the Ro population was significantly higher ($P<0.05$) than that of the Pa population.

TABLE 3.3

Mean maximum population density (eggs/ml) attained by Pa and Ro in field microplots.

Species	n	mean	(±SE)
Pa	16	283.2	(±12.5)
Ro	14	404.1	(±24.7)

The maximum density attained by both species was not sustained in subsequent generations and in most cases later post-harvest levels were below the pre-plant level.

Equilibrium points were calculated for Pa and Ro at 307 ±SE 1.7 and 321 ±SE 37.4 respectively. These values were not significantly different from each other ($P>0.05$) and were obtained from selected individual pre-plant densities that had multiplication rates approaching unity (± 0.1). Equilibrium values for both species are shown in Figure 3.1.

There was considerable variation in the pre-plant densities which gave rise to this low multiplication rate and is reflected in the different location of plotted and calculated equilibrium points (Figure 3.1).

Multiplication rates for both species over a range of pre-plant densities were calculated. The change in multiplication rate with increasing density was exponential and for analysis the initial density and multiplication rate were transformed to a logarithmic scale (log10) (Figure 3.2).

Linear regressions were performed on these transformed data and significant fits were obtained ($P<0.05$).

FIGURE 3.1

The relationship between log pre-planting densities and log post-harvest densities from the 1981-82 experiments with pre-plant densities of 3, 10, 50, 100, 150 eggs/ml of soil.
Equilibrium point (Eq) calculated from selected populations of the 1979-80 and 1980-81 experiments with pre-plant densities that had increases in density approaching unity.
Calculated Eq Pa = 307 eggs/ml (log 5.72)
Ro = 321 eggs/ml (log 5.77)

swiss cross	=	Equilibrium point
circles	=	Ro
triangles	=	Pa
solid line	=	Ro fitted line
short dashed line	=	Pa fitted line
long dashed line	=	non response line (a=1)

(smoothed line fitted by eye).

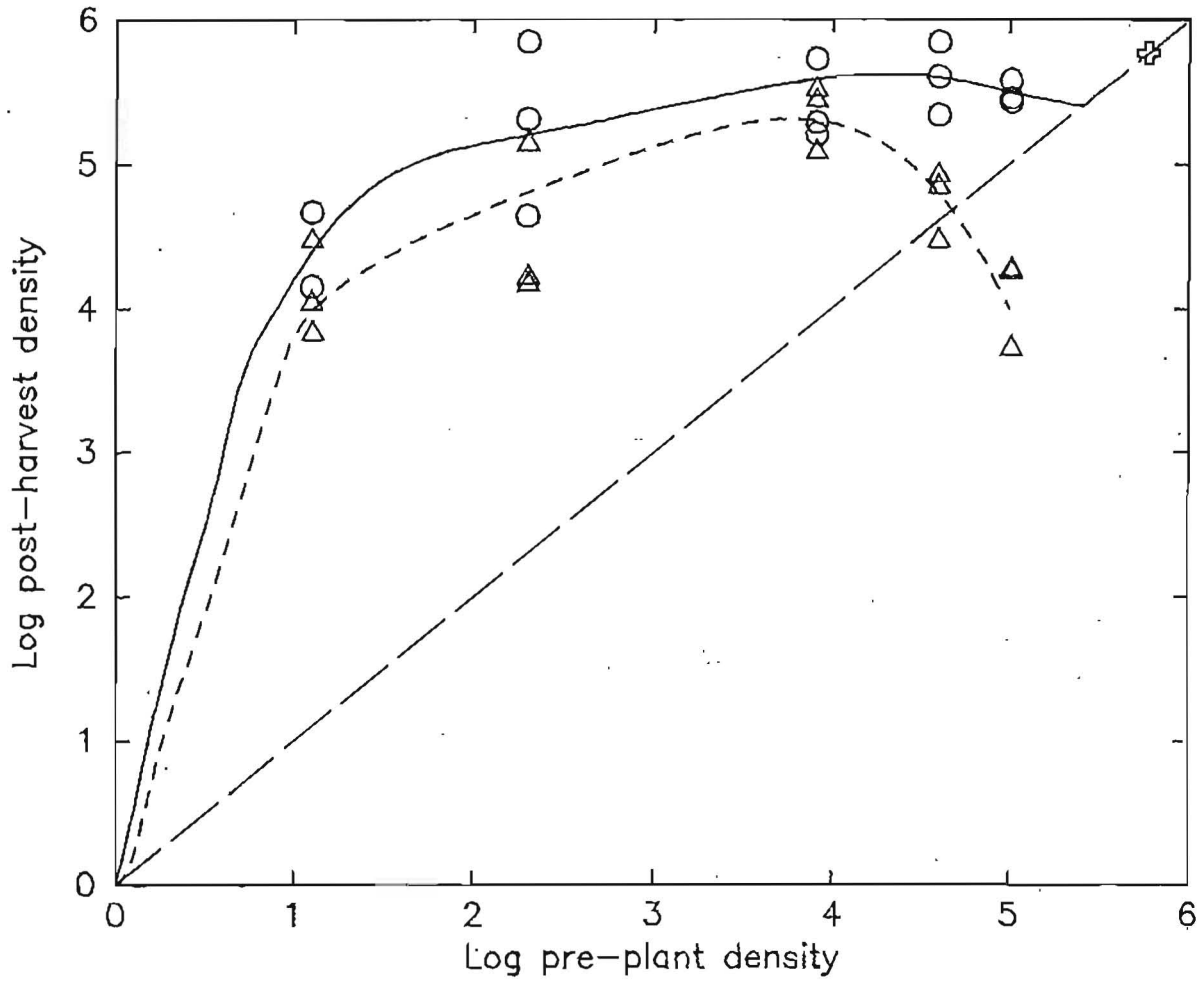

Log post−harvest density
Log pre−plant density
0
1
2
3
4
5
6

FIGURE 3.2

The density dependent relationship between multiplication factor and initial density of viable eggs (eggs/ml soil) for both Pa and Ro.

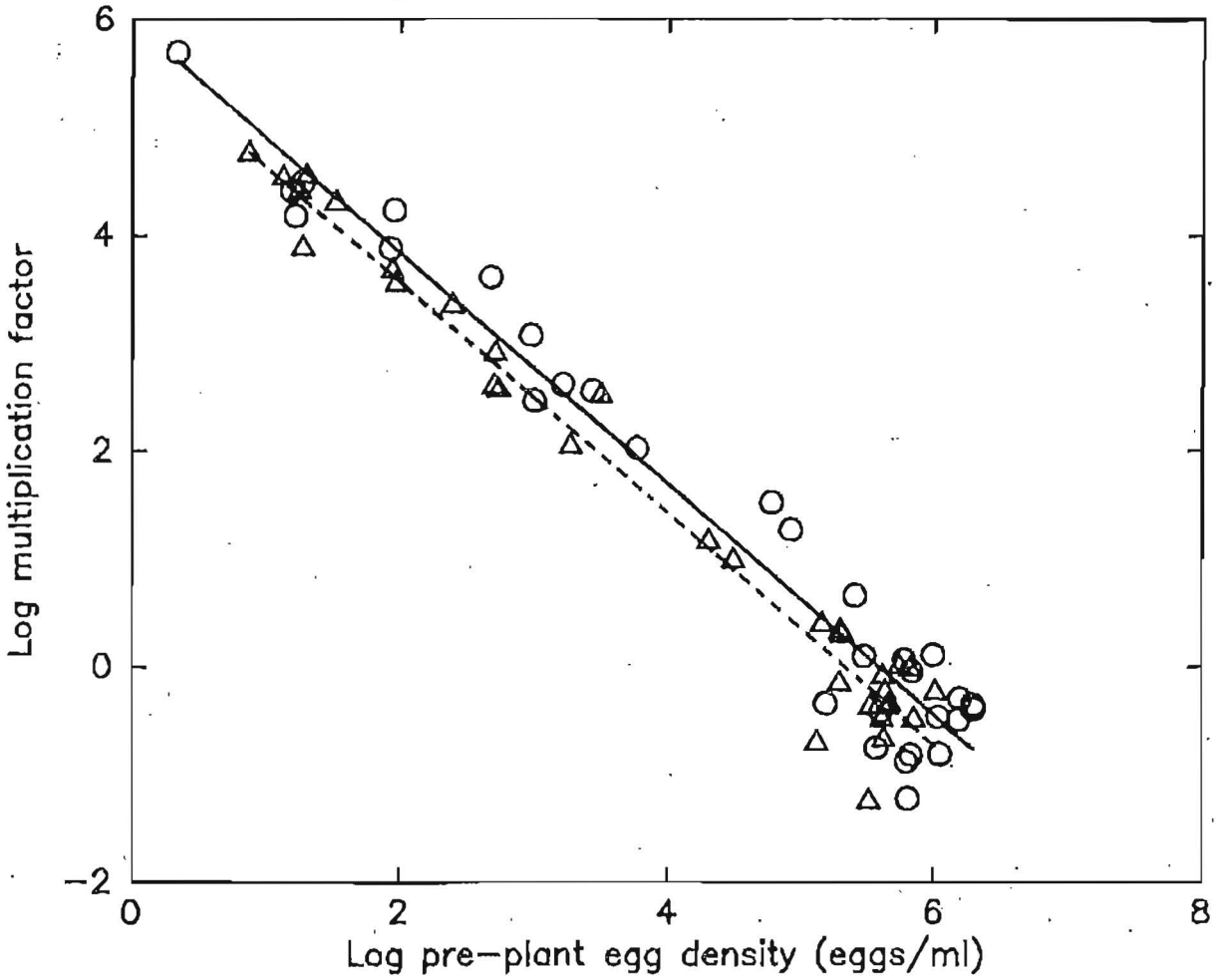
(Straight lines fitted by least squares line of best fit).

circles	=	Ro
triangles	=	Pa
solid line	=	fitted regression line Ro
short dashed line	=	fitted regression line Pa

Regression equations

$$Pa = 302 \times Pi^{-107}$$
$$Ro = 397 \times Pi^{-107}$$

Pi = pre-plant density


Log multiplication factor
6
4
2
0
−2
0
2
4
6
8
Log pre−plant egg density (eggs/ml)

There was no significant difference in the slopes of the regression lines for the two species but Ro had a significantly ($P<0.05$) higher multiplication rate than Pa (mean difference 0.27 ± 0.01). From the regression equations it is possible to calculate an expected multiplication rate for a given initial density within certain limits (Oostenbrink, 1966).

3.3.2 Relationship between initial density and yield loss.

Mean yield and numbers of table and seed sized tubers (> and < 100g, respectively) from infested and control microplots are shown in Appendices V and VI.

The results from infested plots were converted to percent loss relative to the control. This eliminated seasonal variations in yield and allowed for direct comparison of all results.

Percent loss of tuber weight and numbers for table and seed sizes are plotted against the log of the pre-plant density in Figure 3.3. Regression analysis showed that over a range of pre-plant densities both Pa and Ro produced a similar host response.

Subsequent analysis of the combined Pa and Ro data showed that a good fit with r values greater that 70% (Table 3.4) was obtained for table weights and numbers but the relationship between changes in seed weight and increasing nematode numbers was not well defined with r values between 27.2 and 28.4%.

As the density of nematodes increased there was a reduction in total weight of tubers, this percentage loss became significant ($P<0.05$) at densities greater than 15-20 eggs/ml.

Loss as a result of nematode attack was reflected in decreased yields of both table and seed size classes. At densities below 20 eggs/ml the percent loss was generally greater in the seed size class than the table class. However, as the density of nematodes increased the percent loss of seed stabilised but the table size class suffered increasing losses until an upper limit of 85-90% loss was sustained.

Loss in tuber numbers followed the same trends as tuber weights and there was an overall reduction in the total numbers of tubers formed with increasing egg density. The greatest reduction in numbers occurred in table sized tubers.

FIGURE 3.3

Observed values for percentage loss in tuber weight and numbers, for table, seed and total tuber size classes with increasing pre-plant nematode density (Pa and Ro values combined). Lines fitted by least squares.

A = table weight B = table number C = seed weight D = seed number
E = total weight F = total number.

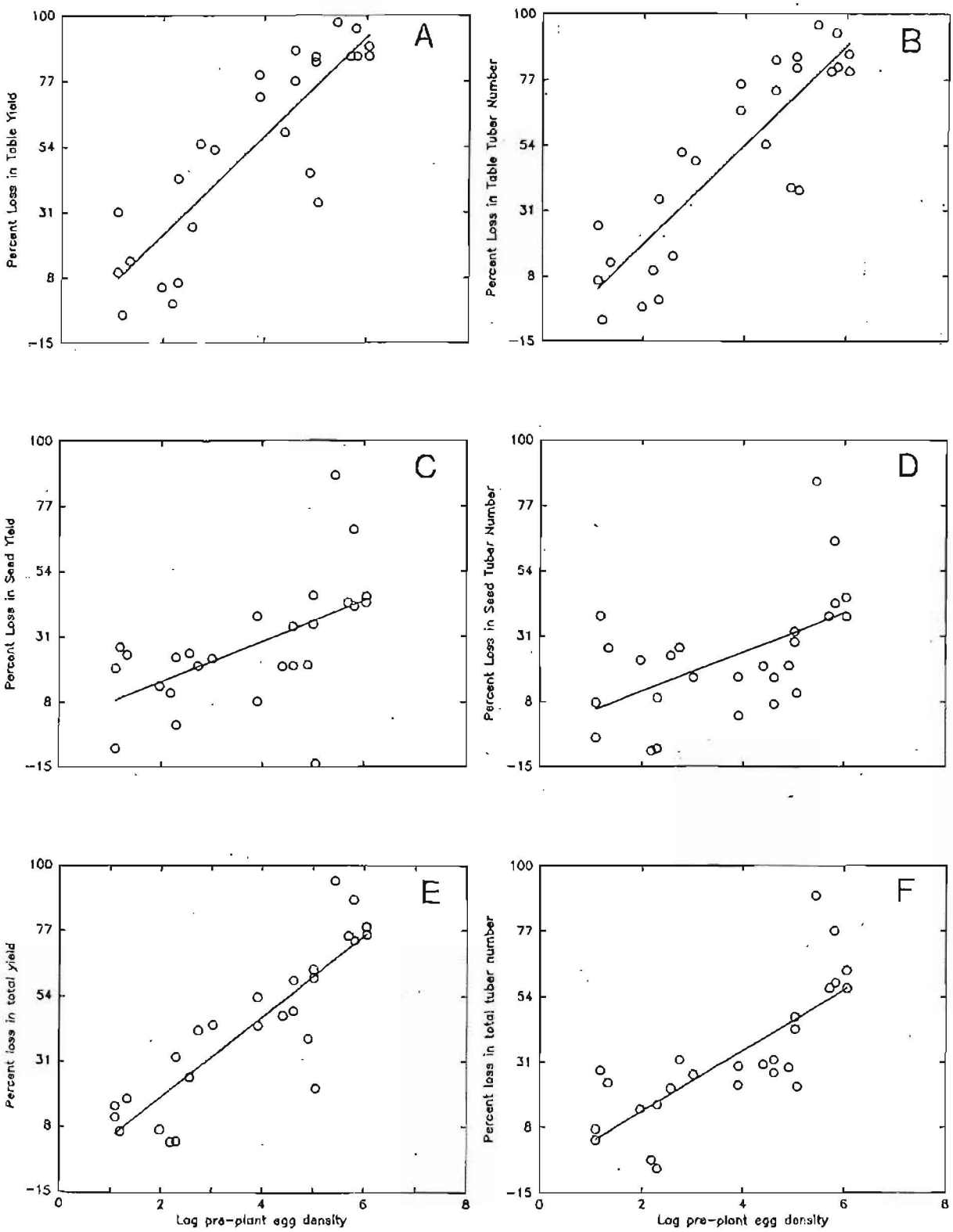

A
B
C
D
E
F
Percent Loss in Table Yield
Percent Loss in Table Tuber Number
Percent Loss in Seed Yield
Percent Loss in Seed Tuber Number
Percent loss in total yield
Percent loss in total tuber number
Log pre-plant egg density
Log pre-plant egg density
100
77
54
31
8
-15
0
2
4
6
8

TABLE 3.4

Intercept and regression coefficients of linear regression equations relating percent loss of yield (for all tuber size classes and numbers) to log of the pre-plant nematode density. (Analysis performed on combined Pa and Ro data.).

Size class	Intercept	Slope	r
Table weight	-10.9	17.169	73.3
Seed weight	-1.01	7.08	28.4
Total weight	-9.65	14.11	56.4
Table No.	-14.9	17.28	75.2
Seed No.	-2.13	6.87	27.2
Total No.	-7.86	10.74	59.7

3.4 DISCUSSION

The use of replicate microplots with a range of initial densities was an effective technique for obtaining field based population and host response data. A wide range of nematode densities and repeated cropping of host plants allowed population development to be monitored over a relatively short time scale.

Populations of both species increased rapidly when introduced into a new environment.

The increase in nematode numbers shown in Figure 3.1 is typical of those described in other published works (Den Ouden and Seinhorst, 1965; Seinhorst, 1966, 1967a, 1967b; Winslow and McKenna, 1973). My study showed that there were significant differences in the biology of the two species as the "ceiling level" (Jones, 1956) and multiplication rate was higher for Ro than Pa. Examination of the observed differences is described in detail in Chapter 5. The equilibrium point on the other hand was similar for both species and suggests that the ability of the host to support the population strongly influences the multiplication of the population especially at high pre-plant levels.

The effect of nematode attack on the potato plant has been extensively examined by Trudgill et al. (1975a, 1975b) and Evans et al. (1977). They found that nematode attack slowed root development and reduced overall root system size which in turn influenced the rate of nutrient uptake. Bird and Loveys (1975) working with Meloidogyne were able to show that the developing females utilized large amounts of plant photosynthetic product when producing eggs. Foot (1978b) found that at high nematode density the mortality of developing adults was higher than at low nematode densities.

These results indicate that density dependent responses evident at lower densities (Figure 3.2; Jones and Kempton, 1978) are modified at higher densities by the capacity of the host plant to grow and to supply the nutrients necessary to enable complete development of the parasites.

Multiplication rates for both species were clearly log-linear over the range of densities examined, but calculation of multiplication rates from initial densities below 3 eggs/ml of soil showed that the linear model tends to over estimate multiplication rate. This could be a result of under population effects in which a dispersed low density population was not able to realise its full reproductive potential. Such effects have been observed by Kort (1962) and Seinhorst (1968). Alternatively it could be the result of distortions produced by the analysis of

logarithmically transformed data. Van der Plank (1975) and Wallace (1973) have commented on this problem, but in the present study it was not possible to determine which was the most likely explanation. At the other end of the density scale, (above 350-400 eggs/ml) multiplication rates decrease to 1x or less and do not fit the log-linear relationship. This deviation is most likely the result of the host response commented on in the previous paragraph. Between the lower and upper densities the log-linear relationship adequately describes the relationship between multiplication rates and initial nematode density.

At the end of the experiment the nematode populations in the microplot were approaching an equilibrum state, although population oscillations (Jones and Kempton, 1978) had not been produced. Development of the population with an initial 'over shoot' followed by a reduction to the equilibrum level suggests that this Canterbury population was no different from those examined by Jones and Parrott (1969) and Jones (1974). Jones and Parrott (1969) suggested that the damped equilibrium (characterised by small scale oscillations about a mean) was largely the result of reduced root size (ie carrying capacity of host) balanced against a reduced population density.

The relationship between nematode numbers and yield losses were identical for Pa and Ro. A log-linear relationship between percent loss in table tuber weight and numbers, and log of the initial nematode density was found. A similar relationship was established for the total yield (weight and number) but seed tuber weight and nematode numbers did not show the same relationship.

Yield loss from nematode damage was significant only above 15-20 eggs/ml of soil. An initial reduction in table and seed tuber weight occurred but losses of the former continued and in the microplots losses of 85-90% were recorded before a yield loss equilibrium was established. This equilibrium level was much higher than the 50% loss level recorded for Pa at Pukekohe (Foot et al., 1980).

3.5 SUMMARY

1. Both Ro and Pa are capable of rapid increases in population density. Increases occurred over a wide range of initial densities until a ceiling level was achieved.

2. The ceiling levels of 283.2 eggs/ml and 404.1 eggs/ml for Pa and Ro respectively were significantly different ($P<0.05$).

3. Equilibrium points for Pa and Ro (307.0 and 321.0 eggs/ml) were calculated and were not significantly different.

4. Multiplication rate was density dependent over the range of initial densities tested, and the log-linear relationship between initial and final densities was maintained over a wide range of densities.

5. Ro had a significantly higher multiplication rate ($P<0.05$) but density dependent responses were the same for both species.

6. Yield loss was related to the pre-plant nematode density and maximum percentage losses reached 85-90% before establishing an equilibrium.

7. There was no difference in host response between Pa and Ro at the same densities.

8. Yield loss was significant above 15-20 eggs/ml of soil with the greatest loss occurring in table sized tubers.

CHAPTER 4

INFLUENCE OF EARLY CROPPING ON A NEMATODE POPULATION

4.1 INTRODUCTION

Potatoes planted in Outram are harvested as an early crop (Chapter 1.3). This practice appears to influence the nematode population as cysts recovered from infested fields are small (250-500 micrometres) and individual cyst fecundity is low (35-50 eggs/cyst). Cyst size in other populations in the South Island is up to 710 micrometres with a fecundity between 150-380 eggs/cyst. At harvest, cysts are white, immature, and easily dislodged from the roots. Despite this, a proportion of the immature (early L_4) male and female population was still imbedded in the root tissue after harvest.

Harvesting methods have become more mechanised and the original hand picking has been replaced by machine harvesting. During the period of handpicking all plants and discarded tubers were removed from the field, but with the advent of machine harvesting most discarded tubers, plant tops and roots are left in the field and incorporated into the soil. A green crop of oats is planted after harvest and within this crop selfset potato plants develop. The potatoes mature before the green crop is ploughed in, in preparation for another crop of early potatoes. Cysts have been found on mature selfsets.

From these observations it was apparent that the production and maintenance of the Outram population is made up of a number of components derived from several sources. The most obvious components were;

(I) immature cysts dislodged into the soil at harvest (hereafter referred to as soil source);

(II) immature L_4 females which develop in the discarded root after harvest (hereafter referred to as root source) and

(III) the residual inoculum carried over from the original cyst inoculum (hereafter referred to as residual source).

In addition, a secondary generation could occur on the selfsets and the inoculum for this generation could come from any or all of the above sources. An experiment was established to examine the contribution of these components and of the selfset generation to the maintenance of the Outram population. A population of unsegregated components was also established and monitored in the same way.

The experiment which was established at Outram in July 1979, ran through two early potato crop cycles and was terminated in May 1981.

4.2 METHODS

4.2.1 Experimental design

Fifty 2.0 litre terylene bags (Chapter 2.5.1) were filled with uninfested Outram soil and inoculated with the equivalent of 20 eggs/ml of Outram produced cysts. This inoculum was contained in eight sachets (Chapter 2.6.1) distributed around a sprouted 50-100 g Ilam Hardy seed tuber. An additional 24 bags inoculated with 10 eggs/ml of soil were set up in the same way, but during the growing season they were sacrificed to determine the tuber bulking rate and an appropriate harvesting date for the original 50 bags. All 50 bags were harvested in November 1979 when the tubers had bulked to a commercially acceptable size. The sacrificial bags also supplied data for life table studies the results of which are presented in Chapter 5.

At harvest, the tops of the plants in each of the 50 2.0 litre terylene bags were clipped off, discarded and the bags emptied. The original inoculum sachets were retained as were the tubers. Each plant root system was vigorously knocked against the side of a 20 litre bucket to simulate mechanical harvesting. The soil, dislodged cysts, and the thrashed roots were collected and retained.

4.2.2 Population components

The harvesting operation produced three population components:

(I) Immature cysts in soil (soil source).

(II) Immature males and females in the host root system (root source).

(III) Residual eggs in the original cyst inoculum (residual source).

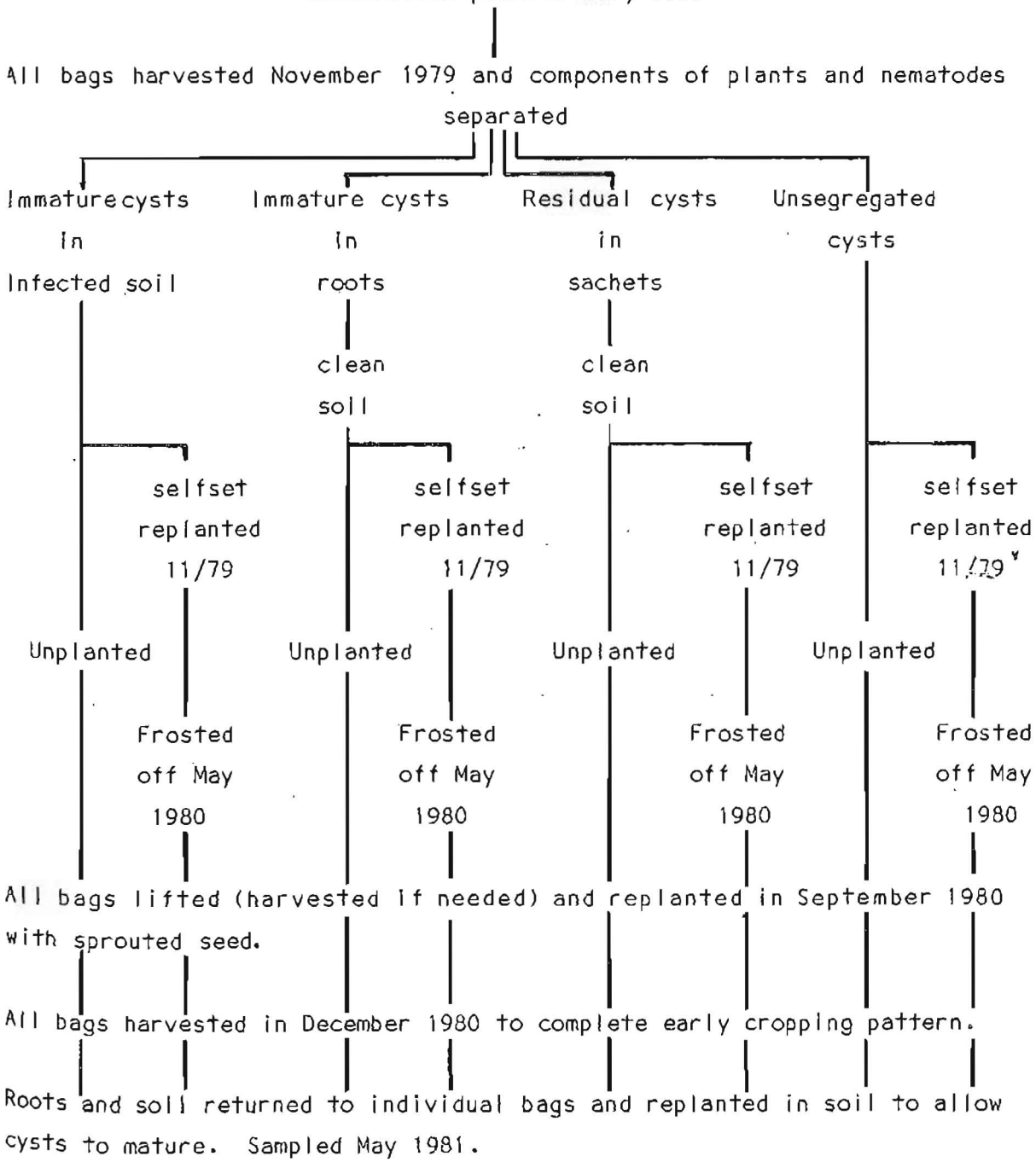
At harvest, the components were separated and the nematode status of each was monitored for a complete cropping cycle both in the presence and absence of a selfset generation between the main cropping cycle.

A flow diagram constructed to illustrate the combinations and time sequence of the experiment is show in Figure 4.1.

In addition to the component treatments, 10 bags containing the unsegregated components were set up both for a single generation and for a selfset generation. The bags were processed in the same way as the main experiment.

FIGURE 4.1

Flow diagram showing the experimental design used to investigate the influence of inoculum source on multiplication of potato cyst nematode at Outram.



Soil source

All infested soil was mixed and rebagged into 10, 20 litre terylene bags. Five of these bags were planted with a freshly harvested 50-100 g tuber which simulated the presence of a selfset plant that could develop after harvest. The five unplanted bags monitored the population under a single cropping system in the absence of selfsets.

Root source

As the number of females in the root could not be determined in the field and to avoid subsequent sampling errors because of low density populations, these were rebagged at the rate of two root systems per 2.0 litres of uninfested Outram soil. Once again five bags were planted with a freshly harvested seed-sized potato tuber and the other five bags in the treatment remained unplanted.

Residual source

Twenty sachets with the residual egg content of the original cysts were rebagged in 10, 2.0 litre bags containing uninfested Outram soil and in keeping with the other treatments half of the bags were replanted with a freshly harvested tuber.

4.2.3 Monitoring population levels of components.

It was not possible to measure initial densities as eggs/ml of soil when the component section of the experiment was established, as the viability of the immature cysts in the soil source could not be determined (Chapter 2.7.3). The number of females in the discarded root source was not determined either as it was not known how many would have survived the trauma of early harvesting. Therefore, the final density (eggs/ml) was determined in September 1980 (Figure 4.1) from component treatments without selfsets and this value was used as the initial density for calculating the multiplication of the same component treatment but in the presence of a selfset tuber.

In September 1980 all 10 bags of each treatment were emptied, tubers were removed, and soil mixed and replaced in clean 2.0 litre terylene bags. From every bag in the experiment a 100 ml soil sample was taken and mean egg density was determined. At this time (September 1980) a sprouted 50-100 g seed tuber was planted in each bag and the experiment was replaced in the field as before. As in the first planting a sacrificial set of bags was used to determine the harvesting date for the experiment. Tubers were not of a commercial size until the first week of December 1980. At this time all plants in each treatment were harvested.

The tops were clipped off and discarded as were the tubers but the roots were thrashed against the bucket and recombined with the soil. The soil plus root from each treatment replicate was rebagged separately and held until May 1981 when final egg density was calculated from a 100 ml subsample from each bag. The root system had decayed by this time and all cysts within the root and in the soil had matured. This enabled viable egg numbers to be determined.

4.3 RESULTS

The number of cysts and cyst fecundity were determined for each treatment in the experiment (Figure 4.1). From these data mean survival, and multiplication factors were calculated and are presented in Tables 4.1 and 4.2.

4.3.1 Single generation effect

Table 4.1 shows survival, fecundity and multiplication factor for three nematode components when exposed to a single crop per year. Table 4.2 has the same format but the effect of a selfset generation in between the two early crops is included.

Female survival (number of eggs introduced as inoculum divided by the number of cysts produced) differed significantly ($P<0.05$) between residual source sachet and both soil and root source derived treatments. However, there was no significant difference in female survival between soil and root source treatments.

Fecundity (eggs/cyst) was generally low with cysts derived from the root source treatments being the lowest (59.4 eggs/cyst). Cysts derived from soil source treatment had an intermediate fecundity (76.5 eggs/cyst).

In all treatments the fecundity of cysts produced was similar to that in the initial inoculum except for the residual source in the sachets. Multiplication (female survival times fecundity) reflected female survival so there was significantly less ($P<0.05$) multiplication in the residual source treatment (5.5x) than in the other treatments which were not significantly different from each other (a mean multiplication factor of (29.1x).

4.3.2 Selfset effect

The effect of a selfset generation which occurred between potato crops in the normal potato/green crop cropping pattern is shown in Table 4.2.

Inclusion of selfsets stimulated hatching and larval development in the soil and from residual sources. In the soil source treatment an overall increase in egg density in the soil (eggs/ml) was found but because of a highly variable response between replicates no significant differences could be demonstrated. The number of cysts present also increased but again the numbers present were highly variable.

The final density (eggs/ml) of each treatment produced from the selfset generation was used as the initial inoculum for subsequent second crop plantings. After harvest, changes in the fecundity, eggs/ml and cyst numbers/100 ml of soil were determined.

The progeny of the selfset generation when used as inoculum for the second early planting experiment gave rise to a population which showed a marked increase in female survival compared to that produced by the selfset generation. However, when compared with female survival in the single generation experiment there were no great differences except that progeny derived from the residual source treatment after a selfset generation had the highest survival of all treatments. Fecundity of cysts produced from the selfset progeny treatment was significantly ($P<0.05$) higher (140.9 eggs/cyst) than in cysts produced in the soil and root source treatments (37.4-46.6 eggs/cyst respectively). The latter did not differ significantly.

Egg density (eggs/100ml of soil) of the three life history components (Table 4.2) after a selfset generation was compared with the same population after a single annual generation and showed that the selfset generation slightly increased the egg density in the soil source treatment, and depressed it in the residual source treatment.

The second early crop increased the density of all treatments but the populations which were produced from a single generation without the additional selfset generation had a higher final density than those exposed to a selfset generation.

The difference between treatments is shown in Figure 4.2. It is apparent that the inoculum derived from partially mature cysts which were dislodged at harvest made the greatest contribution to the population increase. Cysts that developed in the root made a lesser contribution and the progeny from the residual inoculum had the least impact on population increase.

FIGURE 4.2

The development of nematode populations at Outram and the influence of selfsets on nematode numbers.

circles with solid line	=	root source wthout selfset
circles with dashed line	=	root source with selfset
triangles with solid line	=	soil source without selfset
triangles with dashed line	=	soil source with selfset
diamonds with solid line	=	sachet source without selfset
diamonds with dashed line	=	sachet source with selfset
squares with solid line	=	total source without selfset
squares with dashed line	=	total source with selfset

Planting times are:

1	=	first entry
2	=	selfset
3	=	second entry

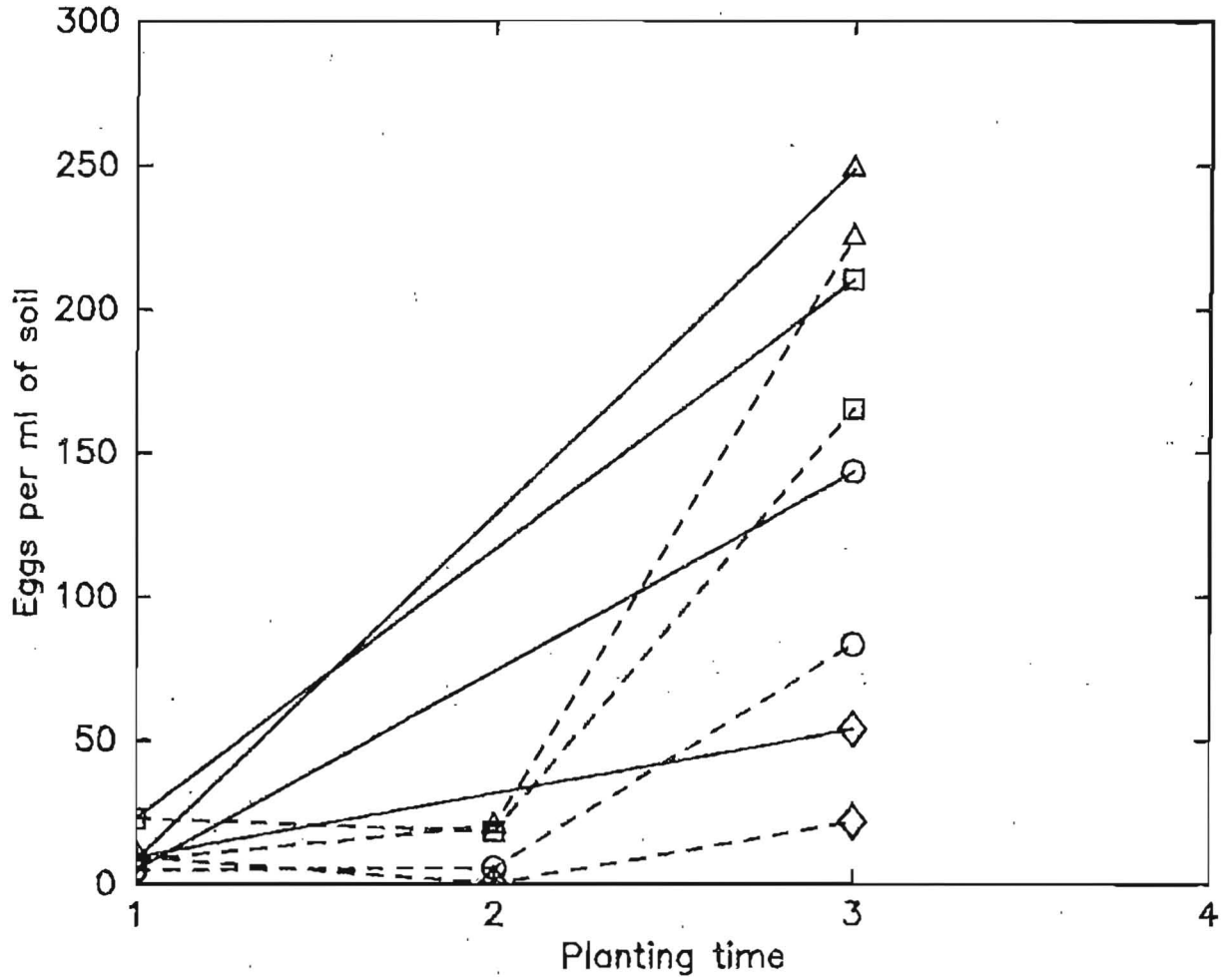

300
250
200
150
100
50
0
Eggs per ml of soil
1
2
3
4
Planting time

TABLE 4.1

Initial and final densities of the three population components and their survival, fecundity and multiplication when exposed to a single crop per year.
(Harvested November 1979 with no selfsets, replanted September 1980 with sprouted seed).

Initial density		Final density		Survival	Fecundity (eggs/cyst)	Multi-plication factor
mean	(SD)	mean	(SD)			
Root source (n=5)						
3.2 eggs/cyst	(5.9)	59.4	(20.8)	0.49a	59.4a	29.0a
5.1 eggs/ml	(2.5)	143.3	(62.5)			
23.2 cysts/100ml	(11.3)	251.2	(116.9)			
Soil source (n=5)						
41.7 eggs/cyst	(4.3)	76.5	(28.4)	0.38a	76.5a	29.2a
8.5 eggs/ml	(2.2)	248.5	(107.0)			
40.3 cysts/100ml	(8.9)	325.0	(120.2)			
Residual source (n=10)						
19.2 eggs/cyst		100.4	(16.4)	0.05b	100.4a	5.5b
9.6 eggs/ml		53.9	(23.8)			
- cysts/100ml		53.5	(21.8)			

Figures with the same letter beside them are not significantly different at the 5% level.

TABLE 4.2

Initial and final densities of the three populations and their survival, fecundity and multiplication when exposed to a selfset generation between the single annual crop.

(Harvested November 1979, replanted with selfsets November 1979. Harvested July 1980, replanted immediately with sprouted seed and finally harvested December 1980.

Initial density		Density after selfset harvest				Multiplication	Density at final harvest				Multiplication
mean	(SD)	mean	(SD)	Survival	Fecundity (eggs/cyst)	factor	mean	(SD)	Survival	Fecundity (eggs/cyst)	factor
Root source (n=5)											
43.7 eggs/cyst	(5.9)	39.8	(11)	0.003b	39.8a	1.1a	46.6	(19.6)	0.32a	46.6a	14.9a
5.1 eggs/ml	(2.5)	5.8	(2.4)				83.3	(34.6)			
11.6 cysts/100ml	(11.3)	14.5	(8.8)				184.0	(26.2)			
Soil source (n=5)											
41.7 eggs/cyst	(4.3)	52.3	(20.2)	0.045a	52.3a	2.3a	37.4	(24.7)	0.26a	37.4a	9.7a
8.5 eggs/ml	(2.2)	20.4	(11.7)				224.8	(176.3)			
20.1 cysts/100ml	4.4	38.8	16.3				536.0	(214)			
Residual source (n=10)											
19.2 eggs/cyst		22.8	(9.2)	0.001b	22.8a	0.03b	140.9	(5.6)	0.67a	140.9b	94.4b
9.6 eggs/ml		0.23	(0.8)				21.8	(8.7)			
- cysts/100ml		1.2	(0.7)				15.4	(5.8)			

4.3.3 Unsegregated population

Unsegregated populations (Table 4.3) with either a single annual generation or an additional selfset generation showed similar patterns for all the component treatments.

The presence of a selfset generation reduced the initial nematode density from 23 to 18.4 eggs/ml. This in itself was not a significant reduction but it did fit the pattern of poor performance observed in the component experiments under a selfset. A single annual generation produced the highest final density of all treatments. Cyst fecundity in the unpartitioned treatments was similar and consistent to the response produced in the component experiments.

TABLE 4.3

Changes in fecundity and density of an unsegregated population when exposed to a single annual crop and a selfset crop (n=5).

Single annual crop	Pre-plant Density	(SD)	Post-harvest Density	(SD)
Fecundity (eggs/cyst)	32.4	(9.6)	60.4	(19.6)
Density (eggs/ml)	23.0	(14.4)	21.0	(88.3)
Multiplication factor			9.1x	

Selfset crop	Pre-plant density	(SD)	Post-harvest selfset Final	(SD)	Final density	(SD)
Fecundity (eggs/cyst)	32.4	(9.6)	45.6	(21.4)	39.4	(6.9)
Density (eggs/ml)	23.0	(14.4)	18.4	(14.0)	165.6	(110.0)
Multiplication factor			0.8x		9.1x	

4.4 DISCUSSION

The production of early potatoes each year at Outram has stressed the cyst nematode population but despite repeated early harvesting it has established and multiplied. Because of limited time for reproduction and maturation the population is of low fecundity and average cyst size is smaller than in other populations infesting main crop potato areas. Although most cysts in the population are outwardly similar in size and fecundity they are produced from different parts of the previous generation.

This situation has occurred because of interrupted reproduction and development of the nematode population when the potato crop was removed. At this time a proportion of the population that had developed to the immature female stage contained non-embryonated eggs. These females were dislodged from the root surface at harvest, fell into the soil and produced mature embryonated cysts in the absence of a supporting host. Embedded within the discarded root system, a smaller but less well developed proportion of the population was also present. This contained both early L_4 males and females. If an infested root was incorporated in the soil after harvest it persisted long enough for the females to develop, be fertilised and mature.

Carry over of larvae in the residual inoculum cyst was estimated to be about 20%. This residue when stimulated by the second early potato crop hatched completely but the female survival rate was significantly ($P<0.05$) lower than those of soil and root sources and show that the residual population was not as vigorous as a comparable number of previously unstimulated larvae. As a survival strategy they had great value as a "second chance" or insurance mechanism in the event of a complete failure of the bulk of the population and their lowered vitality is probably directly related to energy resources within the L_2. Omidvar (1961) estimated that L_2 with depleted fat reserves had a lower establishment rate than those with a good fat reserve.

Although the developmental status of the soil and root source populations was different, they both had the potential to reproduce after a period of maturation and multiplication and fecundity were very similar.

Multiplication rates for soil and root source populations were good as a result of high female survival, but the residual source inoculum had a low female survival which resulted in low multiplication.

Fecundity of the progeny derived from the residual inoculum source was approximately twice that of the other population sources. The increased number of eggs found suggests that the residual population

either hatched earlier or developed more quickly than the other components.

Selfsets influenced the development of the Outram population and the degree of influence varied according to the inoculum source.

Soil source cysts which fell off the roots at harvest were well developed and had time to mature before the selfsets broke dormancy, produced roots and stimulated the larvae to hatch. Female survival of the selfset generation was lower than in the early single crop generation which is not surprising as the soil temperature was high (Appendix VII) and soil moisture was lower (Appendix VII) in late January when the larvae would be present in the soil. Once in the root, normal development was possible until the host was killed by frost. At this stage it appeared that the population was sufficiently well advanced to enable females to mature and eggs to develop.

Cysts produced from the root source were not stimulated to hatch by the presence of selfsets and it is felt that this lack of response reflected the immaturity of the population.

Selfsets also stimulated the contents of residual cysts but female survival was very low compared to female survival in soil and root sources. Those larvae that were successful established in the host root and produced a few cysts that had almost half the fecundity of those from the other inoculum sources. From this it appears that the residual population is not conditioned to respond to selfset stimulation and does so only when the selfsets are well advanced. This conclusion is based on the low level of cyst fecundity which showed that egg development was less advanced before the host died. A generation on a selfset host is largely detrimental to the residual larvae in the cyst but it transforms a low fecundity vestigal population into a higher fecundity population although at the cost of lowering the final density. For all inoculum sources the presence of a selfset generation is not as productive as a single generation based on an early potato crop.

When exposed to an early potato crop the progeny of the selfset generation were stimulated to hatch, reproduce and multiply and were no different from the population produced from a single annual crop regime. There was no significant difference in fecundity, female survival or multiplication rate for root and soil sources. However, the progeny derived from residual larvae in the primary inoculum had a significantly ($P<0.05$) higher survival, fecundity and multiplication rate than those from the other two sources. This was largely a consequence of a lower initial density of inoculum which allowed a full utilisation of prime .pa feeding sites and resulted in a greater proportion of females in the

population and a greater multiplication rate.

The contribution of the population components to the overall density in the soil was highest for the soil source inoculum followed closely by the root source inoculum. The residual source though starting from a similar initial density made a much smaller contribution. The comparable unpartitioned population had a lower multiplication which was probably the result of higher initial density and resulting, density dependent processes. The inoculum mixture with different reproductive capacity should also have had an effect. There was no great difference between the fecundity of the final population in the partitioned and non-partitioned populations.

The similarity in the fecundity of the populations developed from the two sources was remarkable as the soil source cysts developed in the absence of supporting hosts and relied on the resources of the female. The number of larvae developed by free females was limited to the number of eggs produced at the time of harvest. These eggs appeared to develop at the expense of other less well developed egg material. On the other hand, at harvest the root source material was still embedded in the root tissue, but was capable of developing into mature females with eggs before the root tissue disintegrated. There is no evidence for any genetic limitation of fecundity because when allowed to develop to full maturity without removal of the host, the same population had a much higher fecundity (Chapter 5.3.4).

4.5 CONCLUSION

The Outram nematode population has developed under suboptimal conditions associated with early planting and early harvesting of the host potato crop. Early harvesting of potatoes produced two developmentally different groups in the population: one derived from early maturing females which are dislodged at harvest and mature in the soil without the host; and another group derived from the less well developed fraction of the population which at harvest is still embedded in the host root. This latter population developed on the moribund roots. Inoculum carry over from the original cyst was also present and constituted a third inoculum type. The chance introduction of selfset tubers stimulated hatch in both the soil derived progeny and the residual inoculum. Female survival on selfsets was generally low and multiplication insignificant. The root source inoculum was not stimulated to hatch by the selfsets. A second crop of early potatoes stimulated all components. Survival and fecundity were similar for all inoculum sources and differences in multiplication were most likely a

consequence of different initial densities. The residual source however, has a much higher cyst fecundity and influenced the multiplication rate.

4.6 SUMMARY

1. Outram population development is restrained by the early harvesting of the host plant.

2. Because of interrupted female development, fecundity of cysts is low (mean 52 eggs/cyst).

3. At harvest a population can be separated into three major groups:-

   (I) Advanced females that fall off the root and continue to develop in the absence of a sustaining host.

   (II) Immature (L_3 and L_4) larvae still imbedded in the host root at harvest which develop to maturity on moribund roots.

   (III) A residual population which is carried over in the initial inoculum cysts and can represent up to 20% of the original inoculum.

4. Selfsets grow after harvest and stimulate hatch in soil source and residual inoculum cysts.

   (I) The selfset generation has low female survival and multiplication.

   (II) The root source inoculum is largely unstimulated by selfsets.

5. Soil source cysts make the greatest contribution to the maintenance of the Outram population followed by root sources. Residual inoculum has a limited impact on population increase.

CHAPTER 5

LIFE TABLE COMPARISONS OF TWO SPECIES

5.1 INTRODUCTION

Several attempts have been made to express mathematically the changes that occur in a population of potato cyst nematodes under different environmental conditions. (Jones, Parrott and Ross, 1967; Seinhorst, 1967a, 1967b). Models based on the logistic equation;

$$\frac{dN}{dt} = rN\left(\frac{K-N}{K}\right)$$

Where N = population size
t = time
r = rate of population growth per capita
K = upper asymptote or maximal value of N

are most widely used and satisfactorily describe the final multiplication of a population from an initial known density (Morris, 1971; Sarakoski, 1976). However, despite modification to account for the observed influences of:

1. partial hatch of the initial population,
2. shifts in sex ratios of the developing population induced by an increase in intraspecific competition as the initial nematode density increases (Ellenby, 1954b; Trudgill, 1967; Ross and Trudgill, 1969; Mugnlery and Fayet, 1981),
3. influence of environmental effects such as soil temperature and moisture (Fenwick, 1951; Ferris and Mai, 1956; McKenna and Winslow, 1972; Stone and Webley, 1975; Hominick, 1979; Foot, 1978b; Franco, 1979).
4. daylength and length of growing season (Ellenby, 1958; Ellenby and Smith, 1975; Franco and Evans, 1979),

the logistic equation does not provide insight into the impact of the above factors on the developing population within the root.

Foot (1978b) examined the relative importance of factors that influence the population dynamics of potato cyst nematodes under different cropping patterns. She recognised and defined four distinct phases or life styles (Table 5.1; Appendix IX) for the potato cyst

nematode and developed a method for drawing up life tables to describe the growth and mortality of a population.

TABLE 5.1

Division of the potato cyst nematode life cycle into life styles and associated entry phases for life table analysis. Life cycle status in the absence of a host, that is cyst quiescence, is not included (after Foot 1978b).

Life style	Entry phase
	1. Effective eggs in initial cohort
A. Within cyst (encysted eggs)	
	2. Second stage juveniles entering soil
B. Within soil (active second stage juveniles)	
	3. Second stage juveniles penetrating root system
C. Within root (feeding juveniles 2nd and 3rd stage)	
	4. Juveniles entering sub-adulthood (fourth stage)
D. Adulthood (sub-adult (4th), and adult stages)	
	5. Breeding adults (based on females becoming mature cysts)

Foot's work is the first successful application of life table methodology to the cyst forming nematodes.

I have used her life style criteria in drawing up life tables for

experimental populations of Ro_4 and Pa_3 produced under two different soil types in Canterbury.

The Outram population was also considered, but because of the different pathotype found there (Ro_1), direct comparisons could not be made with the Canterbury populations. However, the effects of early harvesting date and full maturity of the host plant on the mortality of the population were examined.

5.2 METHODS

5.2.1 Experimental design

Mortality and development of *G. rostochiensis* (Ro_1, Ro_4) and *G. pallida* (Pa_3) were examined under different conditions in three soil types; silt (S4), peat (Cranford St.), silt loam (Outram) (Table 5.2). At each location, experiments were conducted to compare the two species. Initial plantings at Outram (early potatoes grown in silt loam) were made in August 1979 but planting for the initial experiments in silt (S4) and peat (Cranford St.) was deferred (in accordance with local practice) until October 1979. Initially all samples were taken at 14 day intervals as recommended by Foot (1978b). However, it was found that this interval was too long for South Island populations which developed much more rapidly than those at Pukekohe. In Canterbury, white cysts appeared on roots between 28 and 42 days after planting. As a consequence, inadequate data were collected and the initial experiments in silt and peat were abandoned. Fortunately, the weekly sampling program used in silt loams (Outram) provided adequate data for life table purposes. Experiments in silt (S4) and peat (Cranford St.) soils were repeated in 1980 when two planting dates, 15 September and 22 December were chosen to approximate early and late plantings.

The soils at S4 and Cranford St. are normally cool (10-11 °C) and moist (22-26% and 75-90% oven dry weight for S4 and Cranford St. respectively) but after the early plantings had been set up an abnormally dry period occurred. During this time the soil moisture at S4 dropped to 13-18% oven dry weight and at Cranford St. it fell to 58-62%. As a result, plant growth and cyst hatching at S4 in particular were unsatisfactory. Consequently, the early planting experiment was scrapped and begun again on 13 October 1980 after heavy rains had increased soil moisture to 23% oven dry weight. To ensure that cool moist soil conditions were maintained in silt (S4), a 50% - light excluding shade frame was erected over the replanted experiment.

The peat soil (Cranford St.) was not shaded because moisture in the peat soils had not been depleted to the same degree. The second planting date (13 October) was still considered early for planting in the Cranford St. district.

TABLE 5.2

Summary of life table experimental conditions. Code name, season commenced, population density, time of commencement, size of cohort and inoculum containerisation is shown for each treatment. (O = Outram, S4 = S4 Lincoln, C = Cranford St.).

Code	Season	Density eggs/ml	Commence-ment date	Cohort size eggs	cysts	Inoculum containerisation (sachets x cysts)
RoO	Winter	10	15/8/79	24,000	151	8 x 19
PaS4	Early Spring	10	13/10/80	25,000	104	8 x 13
PaC	Early Spring	10	13/10/80	25,000	104	8 x 13
RoS4	Early Spring	10	13/10/80	28,000	151	8 x 18
RoC	Early Spring	10	13/10/80	28,000	151	8 x 18
PaS4	Early Summer	10	22/12/80	25,000	104	8 x 13
PaC	Early Summer	10	22/12/80	25,000	104	8 x 13
RoS4	Early Summer	10	22/12/80	28,000	151	8 x 18
RoC	Early Summer	10	22/12/80	28,000	151	8 x 18

To summarise, successful experimental populations used for life table analysis were set up in silt (S4) and peat (Cranford St.) on 13 October and 22 December 1980 and in silt-loams (Outram) on 15 August 1979.

5.2.2 Cohort/host unit

Potatoes in terylene bags containing standard inoculum (Chapter 2.5.1) were used in the experiments (Table 5.2). The inoculum used at Outram (Ro_1) was collected from an experimentally produced field population at Outram. This inoculum had a residue of the unhatched initial inoculum dispersed throughout the soil with the newly produced cysts. The lower eggs/cyst count of this mixture, compared with inoculum used at S4 and Cranford St. was compensated for by the use of a greater number of cysts. In each cohort/host unit, the inoculum was dispersed throughout the soil except for four cohort/host units that were inoculated with eight replicate sachets containing the same quantity of inoculum. These cohort/host units were used to determine the proportion of egg hatch at the end of the experiment. Because the time needed to complete the experiment was unknown at the start, and because the plants were destructively sampled, 90 inoculated cohort/host units were made up for each species, planting date and location. This permitted a maximum of 22 sampling occasions.

On each sampling date, four cohort/host units for each species were collected from the peat soils (Cranford St.) and silt soils (S4) and processed immediately at the S4 laboratory. Samples from Outram were collected by MAF staff and road-freighted in an insulated box to Lincoln. These samples were processed within 24h of being collected from the field. The Outram samples were collected weekly. S4 and Cranford St. samples were drawn at three and four day intervals until white cysts appeared on the roots. Thereafter, the sampling interval was extended to approximately seven days, but in early plantings, samples were taken at about 14 day intervals after the experiment had run for 70 days.

5.2.3 Parameters measured

Environmental monitoring - A temperature sensor connected to a continuous recorder was inserted 100 mm below the soil surface into the root ball of one growing plant within each experiment (Chapter 2.10). Daily temperatures were calculated from recorded maximum and minimum readings. The simple arithmetic mean soil temperature for the duration of each life style was also calculated.

on each sampling occasion and used for soil moisture determinations (Chapter 2.10). From these measurements the mean soil moisture (% oven dry weight) for each life style was calculated.

Other parameters measured on each sampling day were those detailed by Foot (1978b). Some of her procedures were streamlined however, especially the extraction of larvae from the host roots.

Assumptions and errors implicit in life table analysis have been reviewed extensively by Foot (1978b) and the procedures for collecting data for life table analysis as outlined by her were followed in the current program.

To calculate survival within each of the four life styles of Globodera species, the number of individuals entering each life style and the number reaching reproductive maturity were estimated. These estimates were calculated from a number of parameters monitored during each series (Table 5.3). The census sequence available for analysis consisted of mean values for each parameter measured, plus an estimate of between-unit variation for each (see Appendices X to XIV). The parameters listed in Table 5.3 were calculated as described below.

Number of cysts per bag - Ten counts of the number of cysts per initial inoculum were made. The mean value gave s.

Number of eggs per inoculum cyst ($k_{inoc.}$) and initial egg status (live b_o dead c_o hatched d_o) - replicate samples of 20 cysts were chosen at random during preparation of the inoculum. Cysts were broken open with needles to release the eggs, which were stained with New Blue R (Chapter 2.7.3). Twenty percent of the eggs in each replicate sample were counted and the proportions live, dead, and hatched were measured. Division of the egg count by four produced an estimate of the number of eggs per cyst for each replicate, and the mean over 10 replicates gave $k_{inoc.}$ The proportions b, c, and d for each replicate were obtained directly from the 20% counts, and their means over the 10 replicates gave b_o, c_o, and d_o.

Total cyst content in the cohort inoculum (a) - This was the sum of the estimated total number of cysts/bag, multiplied by the mean number of eggs per cyst ($k_{inoc.}$).

Egg status at sample date n(b_n, c_n, d_n) - At each sample date n, four cohort/host units were uplifted for census. The 15 cysts forming the dispersed inoculum were removed from the soil within each bag, and egg status was assessed as described. This was continued until the new cysts produced on the roots had turned brown and could not be distinguished from the inoculum. At the last sampling date the bags containing the inoculum in sachets were collected to give the final

estimate of egg hatch.

Mean status of the four cohorts provided b_n, c_n, and d_n.

Number of juveniles within the root system at sample date n (f_{1n},f_{2n},f_{3n}, sr_n) - Root systems of each of the four cohort/host units uplifted at sample date n were separated carefully from the 2.5 litres of soil. Fine roots were removed with forceps. Each root system was washed over a 150 micrometre sieve, and the sievings which passed through were returned to the soil which was retained for assessment of adult nematode (i_n) numbers. The washed root system was cut into 20 mm lengths and fixed, stained and stored in clear lactophenol.

Five grams of root/material from each sample were taken at random, washed clean of stain, drained for 60 seconds and examined for nematodes. Because of the number of samples collected during the experiment the manual extraction method used by Foot (1978b) was not feasible. Instead, a combination of mechanical maceration and selective sieving was used as described in Chapter 2.8.2.

The development of each individual was determined and numbers of second (f_1), third (f_2), and fourth (f_3) stage juveniles in the root sample were counted. An individual was classified as being of a particular stadium on a moult to moult basis. Estimates for each total root system were calculated, and the mean value from the four replicates gave f_{1n}, f_{2n}, and f_{3n}.

Sex ratio (sr_n) - The sex of all fourth stage juveniles counted in each sample was determined to provide a cohort sex ratio estimate, sr. The mean value for the four cohorts sampled gave sr_n.

TABLE 5.3

Parameters measured during the life of a cohort of potato cyst nematodes (after Foot, 1978b).

Initial assessment		
s	-	number of cysts per bag
$k_{inoc.}$	-	number of eggs per inoculum cyst
a	-	total cyst content in cohort inoculum
b_o	-	proportion of live eggs in inoculum
c_o	-	proportion of dead eggs in inoculum
d_o	-	proportion of hatched eggs in inoculum
Assessment at each sample date n (= t days from beginning)		
b_n	-	proportion of live eggs in cohort at nth sample date
c_n	-	proportion of dead eggs in cohort
d_n	-	proportion of hatched eggs in cohort
f_{1n}	-	number of second stage juveniles in root system
f_{2n}	-	number of third stage juveniles in root system
f_{3n}	-	number of fourth stage juveniles in root system
sr_n	-	sex ratio ($\frac{\sigma^{\prime}}{\varphi + \sigma^{\prime}}$) of fourth stage juveniles
i_n	-	number of adult females
k_n	-	number of eggs per adult female
Final assessment		
$b_{fin.}$ $c_{fin.}$ $d_{fin.}$	-	Final state of inoculum cysts (proportion of eggs live, dead, and hatched) as a mean calculated from all post-activity sample dates
$i_{fin.}$	-	final number of adult females as a mean calculated from all post-activity sample dates
sr_{tot}	-	overall sex ratio calculated from $\dfrac{\sum_n sr_n \cdot f_{3n}}{\sum_n sr_n \cdot f_{3n} + \sum_n (1-sr_n) \cdot f_{3n}}$
v	-	proportion of live eggs per new cyst (viability of progeny) at final sample date.
p	-	total progeny (new eggs) produced = $i_{fin.} \cdot k_n$
vp	-	total viable progeny produced = $v.p$

Number of adult females (l_n) - Adult females drop off the root during extraction of the root system from the soil of the cohort/host unit. Therefore, for each of the four units sampled at date n, an estimate of adult females (new cysts) was obtained after root extraction. The cohort soil was mixed thoroughly before three, 100 ml samples of soil were taken and immediately placed in 5 litres of water. The new white cysts were decanted off from a tray to a sieve (detailed in Chapter 2.7.2.) and counted. Multiplication of the mean number of cysts per 100 ml by the appropriate factor (total soil volume divided by sample volume) provided an estimate of adult female density in soil. An estimate of the number of adult females still attached to the root, obtained during examination of the sample root for juveniles, was added to this to provide a total estimate of adult females in a cohort. These measurements were discontinued when cyst colour of progeny (l_n) became indistinguishable from that of the inoculum. The mean value over four cohorts gave i_n.

Final values $b_{fin.}$ $c_{fin.}$ $d_{fin.}$ $i_{fin.}$ - Post-activity status of these parameters was defined as the state at which rate of change of the parameter approached unity. For example, where values b_n to b_{n+x} were not significantly different ($P>0.05$), then all unit replicate values used to estimate b_{n+1} to b_{n+x} were combined to provide an overall final estimate $b_{fin.}$ from $4(x-1)$ unit replicates.

Number of eggs per adult female (k_n)

Before the root ball was disturbed, 10 cysts taken at random from a length of root were removed for the estimation of mean female fecundity. The number of eggs/cyst provided a cohort fecundity value. The mean of four cohorts gave k_n.

Overall sex ratio ($sr_{tot.}$) - This was the sex ratio calculated from the estimated total numbers of fourth stage males and fourth stage females present over all sample dates. Summation of individual sample dates was necessary because of a change in sex ratio with time.

Viability of progeny (v) - During estimation of the number of adult females on the final sampling date, the viability of eggs in 20 new cysts (proportion of live eggs) was determined using New Blue R as described earlier. Mean value over the four units gave v.

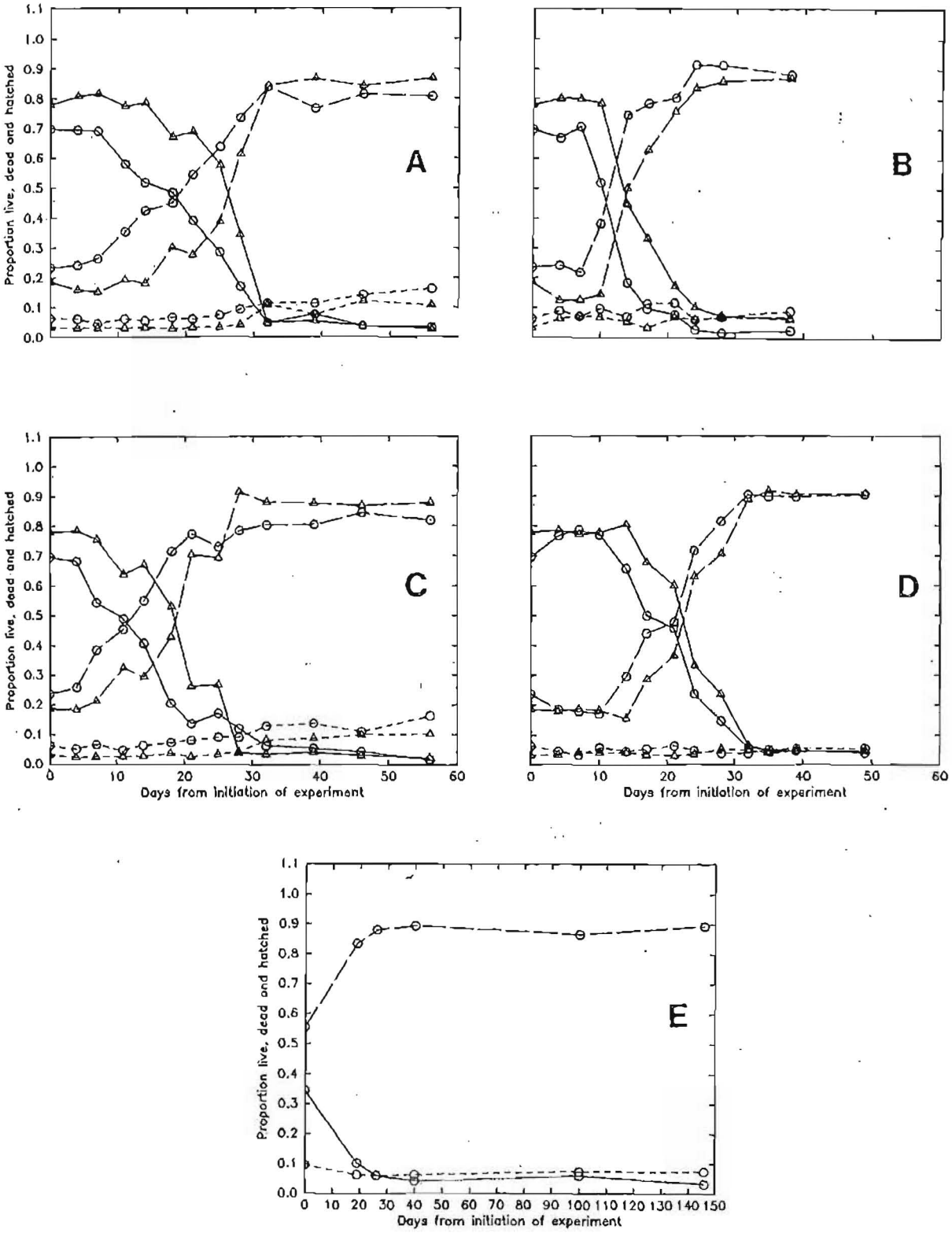
Equations used in the construction of life tables were developed by Foot (1978b) and during this study a computer program was written by Mr. B. Muschamp of Physics and Engineering Laboratory, DSIR, to allow rapid computation of the results. The text equations and formulae used by Foot (1978) have been included in Appendices XV and XVI.

FIGURE 5.1

Inoculum cyst status. The proportion of live eggs (b_n), dead eggs (c_n), and hatched eggs (d_n), in the cysts of G. rostochiensis and G. pallida at three sites and two planting dates are shown.

A = S4 early planting; B = S4 late planting; C = Cranford St. early planting; D = Cranford St. late planting; E = Outram early planting.

solid line	=	live eggs (b_n)
long dashed line	=	hatched eggs (d_n)
short dashed line	=	dead egg (c_n)
circles	=	G. rostochiensis
triangles	=	G. pallida


Proportion live, dead and hatched
A
B
C
D
E
Days from initiation of experiment

5.3 RESULTS

Life table data collected from the five experiments carried out during 1979 - 80, 1980 - 81 are presented in Appendices IX to XIII.

5.3.1 Egg hatching

Hatching of inoculum was consistently high and is shown in Figure 5.1. The final proportion of eggs hatching for both species in different experiments is shown in Table 5.4.

TABLE 5.4

Mean proportion of eggs hatched ($b_{fin.}$) in all experiments.

Experimental conditions	Proportion hatched	
	Ro	Pa
Early planting silts	0.79	0.85
Late planting silts	0.90	0.85
Early planting peats	0.78	0.88
Late planting peats	0.90	0.90
Early planting Outram	0.89	- -

Regardless of planting date and experimental site there was no significant difference ($P>0.05$) in the proportion of eggs that hatched in either species. However, differences in the time taken to hatch were found between species, planting dates and experimental sites and are shown in Table 5.5.

TABLE 5.5

Days elapsed between planting and initiation of egg hatching and mean hatching time for both species in all experiments.

	Ro		Pa	
Experiment	hatch initiation (day)	mean hatching time (days)	hatch initiation (day)	mean hatching time (days)
Early planting silt	8a	20d	18c	25d
Late planting silt	10a	17d	14a	19d
Early planting peat	4b	11ad	7a	17cd
Late planting peat	4b	13ad	7a	14ad
Early planting Outram	-	10ad	-	-

Values with letters in common did not differ significantly at the 5% level

Except for the late plantings in silt (S4), Ro hatched significantly earlier ($P<0.05$) than Pa. Once initiated, hatching took 5 - 12 days. A similar proportion of eggs hatched at Outram (silt/loam) but because of infrequency of sampling the time taken to initiate, hatching was not determined precisely. The mean hatching point of eggs in each experimental situation was calculated from the time of planting ($t=o$) and the end point of egg hatch which occurred at $t=n$. At Outram the mean hatching point occurred earlier than in other populations.

The proportion of dead eggs in the samples did not increase significantly during the course of any experiment, but the mean proportion of post inoculum dead ($dead_{fin.}$ $dead_{inoc.}$) was significantly higher ($P<0.05$) for Ro_4 (0.23) than for Pa (0.19).

5.3.2 Larval development

The frequency of occurrence of the three larval stages, L_2 (f_{1n}) L_3 (f_{2n}) and L_4 (f_{3n} both male and females) (Figure 5.2) over the duration of the experiments is shown in Figures 5.3 5.4 5.5. L_2 larvae were detected early, built up rapidly to peak numbers after 18-32 days and then slowly declined. Development of the Outram population (silt loams) differed from the others in that the L_2 stage persisted for approximately 61 days even though it was present early in potato root development. The transition from L_2 to L_3 larvae and subsequently to the L_4 stage was also slower at the Outram site where completion of the life history took approximately 150 days. This compared with about 60 days elsewhere. The shorter life histories were associated with rapid larval growth indicated by clearly defined L_3 and L_4 peaks.

5.3.3 Sex ratio of L_4 stage larvae

Sex ratios of L_4 larvae of Ro and Pa are shown in Figure 5.6. In all populations females predominated early but the sex ratio changed rapidly with time. The rate of change was similar for both species in each experiment although it differed between sites and planting dates.

Mean overall sex ratios of L_4 larvae of each species under each experimental condition are shown in Table 5.6.

TABLE 5.6

Overall sex ratios (M:F) of L_4 larvae in populations of Ro and Pa grown under each set of environmental conditions.

Experimental condition	Species	
	Ro	Pa
Early planting silt	0.53	0.40
Late planting silt	0.47	0.38
Early planting peat	0.37	0.30
Late planting peat	0.54	0.33
Early planting Outram	0.39	-

FIGURE 5.2

Life cycle of G. rostochiensis and G. pallida (modified from Chitwood and Buhrer, 1946); illustrating the five entry phases and four larval stages used in the life table analysis.

A = entry phase 1, effective eggs in initial cohort; B = entry phase 2, second stage larvae entering soil; C = entry phase 3, second stage larvae penetrating the root; D = entry phase 4, larvae entering sub-adult fourth stage; E = entry phase 5, breeding adults.

Within entry phases 3, 4 and 5 larval stages corresponding to f_1 f_2 f_3 and i develop.

1. Second stage juvenile (f_1); within root and undergoing second moult.
2. Third stage juveniles (f_2); early stage.
3. Third stage juveniles (f_2); late stage and early third moult.
4. Fourth stage juveniles (f_3) males; early stage and late fourth moult.
5. Fourth stage juveniles (f_3) females; early stage and late fourth moult.
6. Adult stage; immature adult female (i) and mature male.

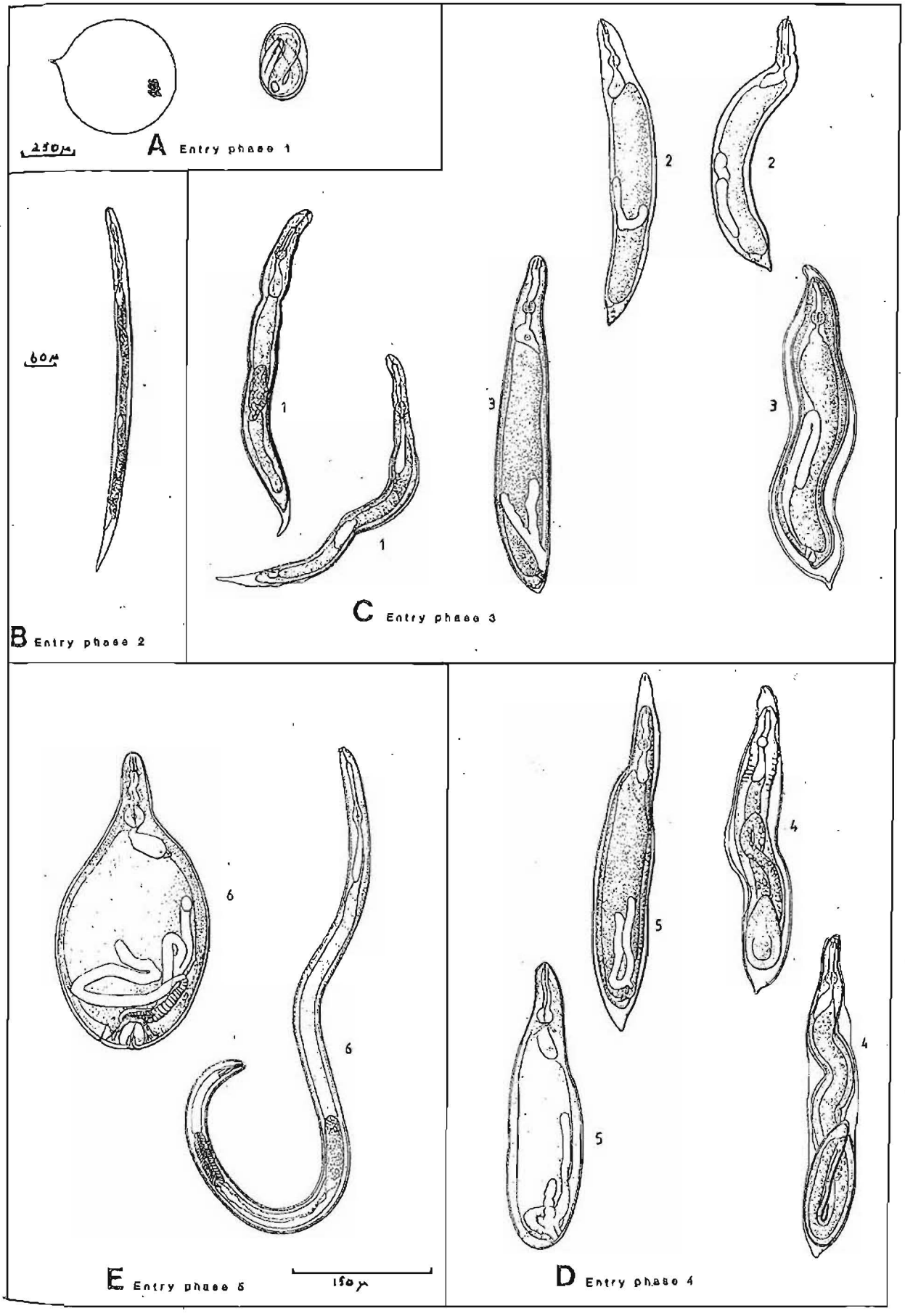

250µ
A Entry phase 1
60µ
B Entry phase 2
1
1
2
2
3
3
C Entry phase 3
6
6
150µ
E Entry phase 5
4
4
5
5
D Entry phase 4

FIGURE 5.3

Frequency of second (f_{1n}), third (f_{2n}) and fourth (f_{3n}) larval stages of G. rostochiensis and G. pallida within roots in silt soils of S4 at two planting dates.

A = early planting with Ro; B = early planting with Pa; C = late planting with Ro; D = late planting with Pa.

solid line = second stage (f_{1n})
short dashed line = third stage (f_{2n})
long dashed line = fourth stage (f_{3n})

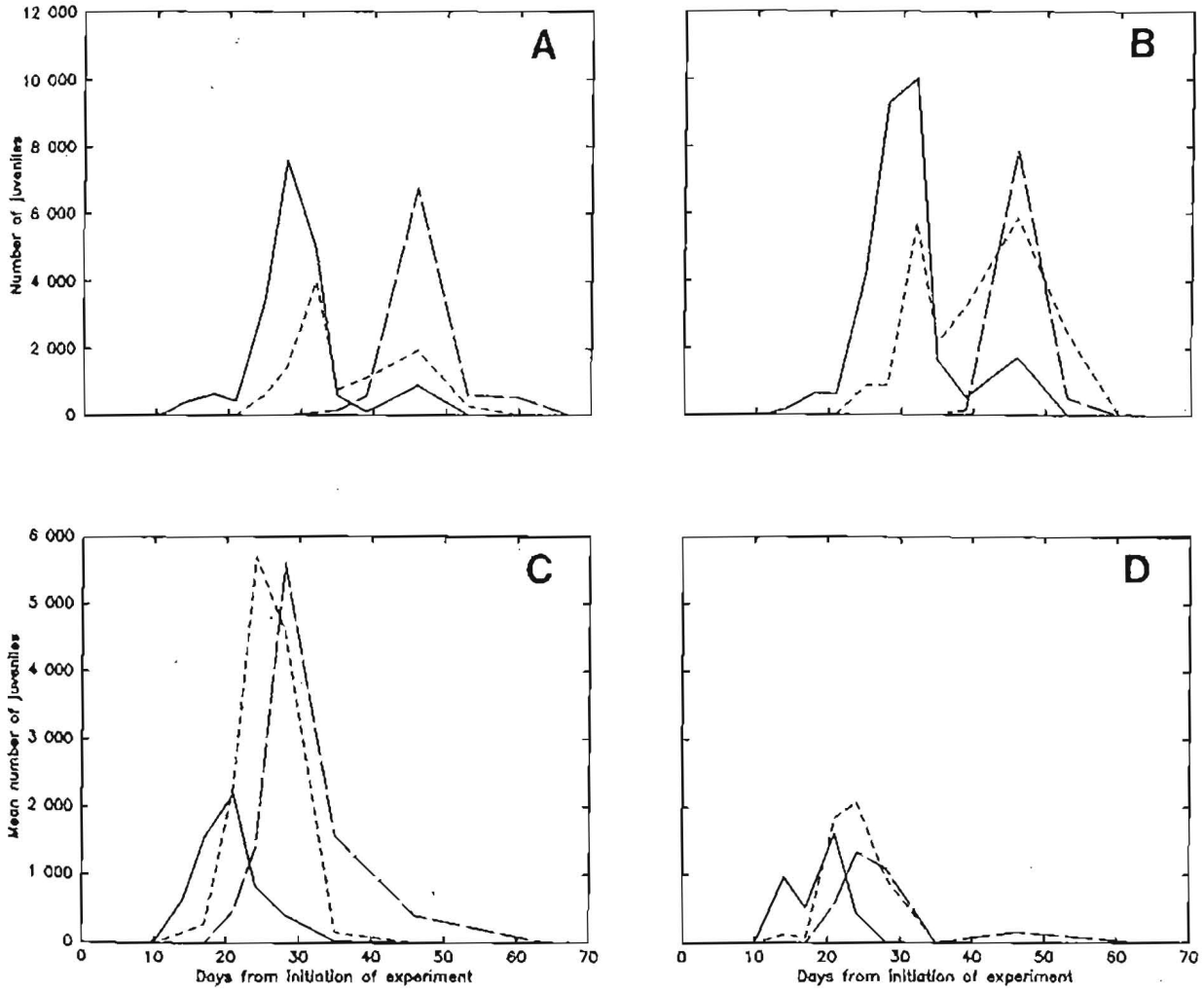

A
B
C
D
Number of juveniles
Mean number of juveniles
Days from initiation of experiment
Days from initiation of experiment
12 000
10 000
8 000
6 000
4 000
2 000
0
6 000
5 000
4 000
3 000
2 000
1 000
0
0
10
20
30
40
50
60
70

FIGURE 5.5

Frequency of second (f_{1n}) third (f_{2n}) fourth (f_{3n}) larval stages of *G. rostochiensis* within roots in silt loams of Outram.

solid line = second stage (f_{1n})
short dashed line = third stage ($_{2n}$)
long dashed line = fourth stage (f_{3n})

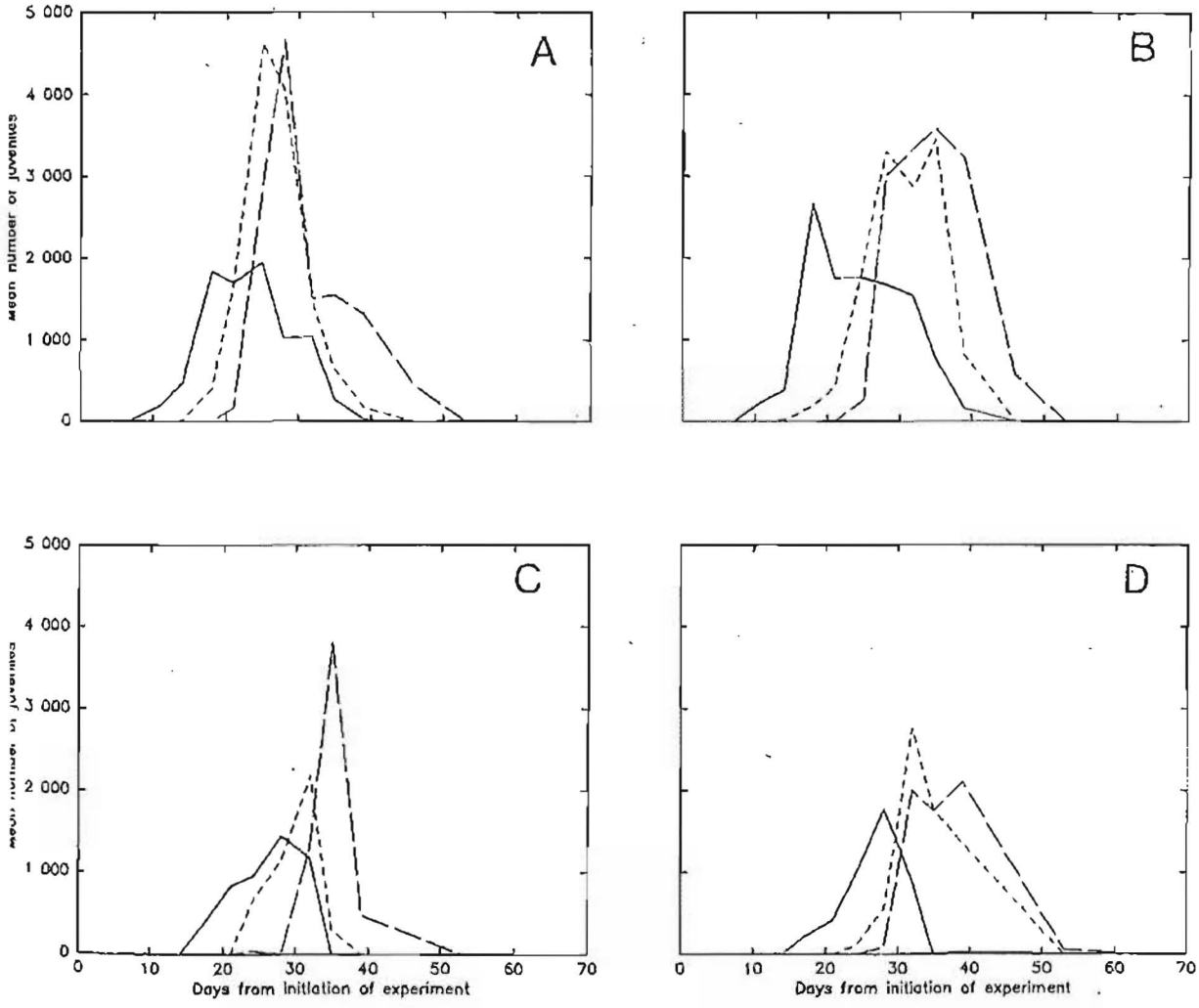

A
B
C
D
5 000
4 000
3 000
2 000
1 000
0
0
10
20
30
40
50
60
70
Days from initiation of experiment

FIGURE 5.4

Frequency of second (f_{1n}), third (f_{2n}) and fourth (f_{3n}) larval stages of *G. rostochiensis* and *G. pallida* within roots in peat soils of Cranford St., at two planting dates.

A = early planting with Ro; B = early planting with Pa; C = late plant with Ro; D = late planting with Pa.

solid line = second stage (f_{1n})
short dashed line = third stage (f_{2n})
long dashed line = fourth stage (f_{3n})

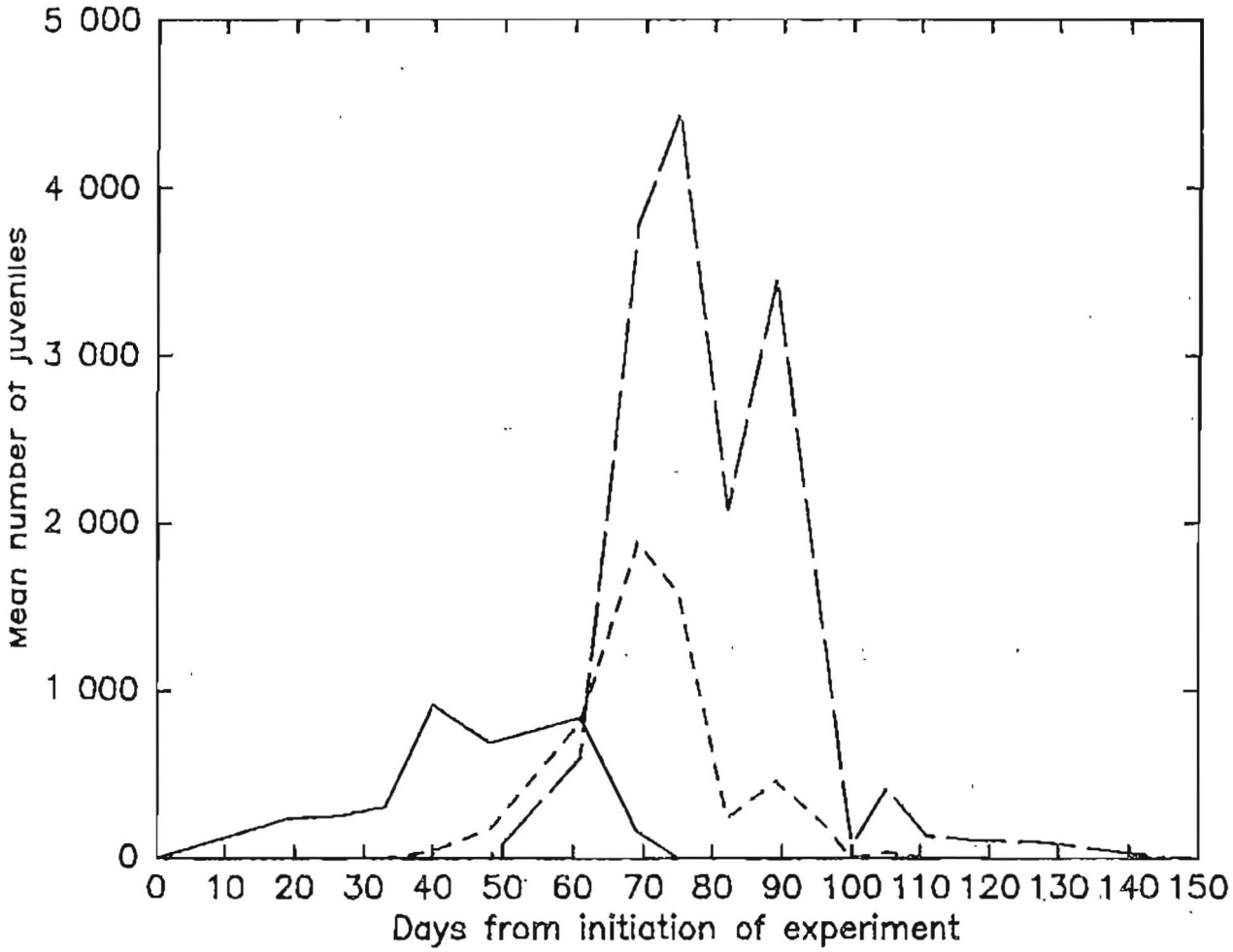
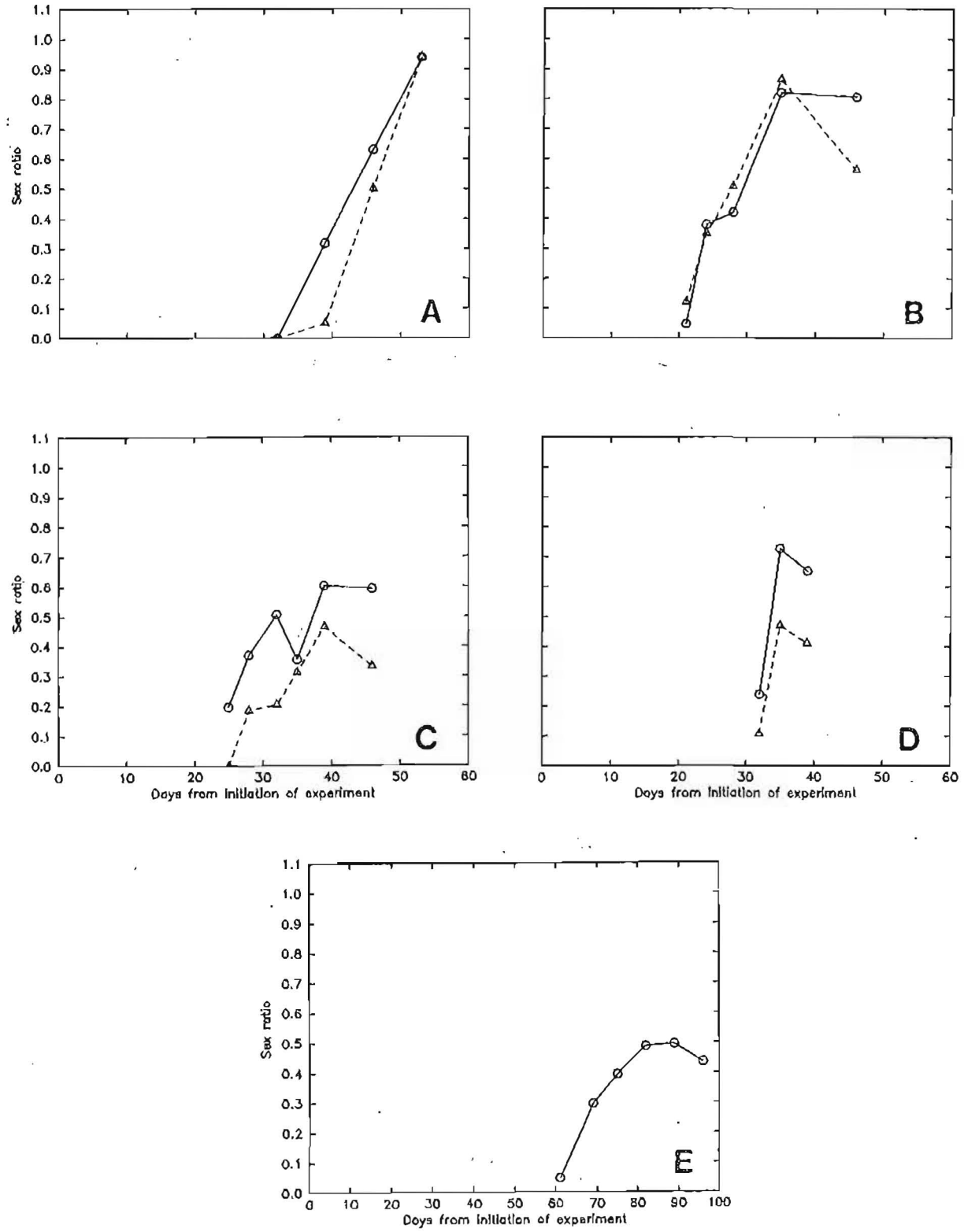

5 000
4 000
3 000
2 000
1 000
0
Mean number of juveniles
0 10 20 30 40 50 60 70 80 90 100 110 120 130 140 150
Days from initiation of experiment

FIGURE 5.6

Sex ratio of fourth stage larvae of *G. rostochiensis* and *G. pallida* at three sites and for two planting dates.

A = S4 early planting; B = S4 late planting; C = Cranford St.; early planting; D = Cranford St., late planting; E = Outram early planting.

circles with solid line = *G. rostochiensis*
triangles with short dashed line = *G. pallida*


Sex ratio
Days from initiation of experiment
A
B
C
D
E

Pa had a higher proportion of females than Ro in all situations but because of the limited sets of paired values (n=4) the data could not be analysed for significant differences. Within each species no significant differences were detected although a trend towards more females in peat soils was apparent.

5.3.4 Cyst fecundity (k_n)

Mean numbers of eggs per cyst were calculated from the developing females (I_n) (Figure 5.7) and are shown in Figure 5.8.

The rate of egg production and final egg numbers per cyst were similar for both species living under the same environmental conditions. However, significant ($P<0.05$) differences were detected between numbers of eggs produced under different environmental conditions (Table 5.7).

TABLE 5.7

Mean numbers of total (live + dead) eggs per cyst found in the two species grown under different experimental conditions.

Experimental condition	Species	
	Ro	Pa
Early planting silt	290 a	260a
Late planting silt	185 b	197b
Early planting peat	244 a	207 ab
Late planting peat	159 b	134 b
Outram early planting		
Early harvest 100 day	44 d	-
Late harvest 150 day	158 d	-

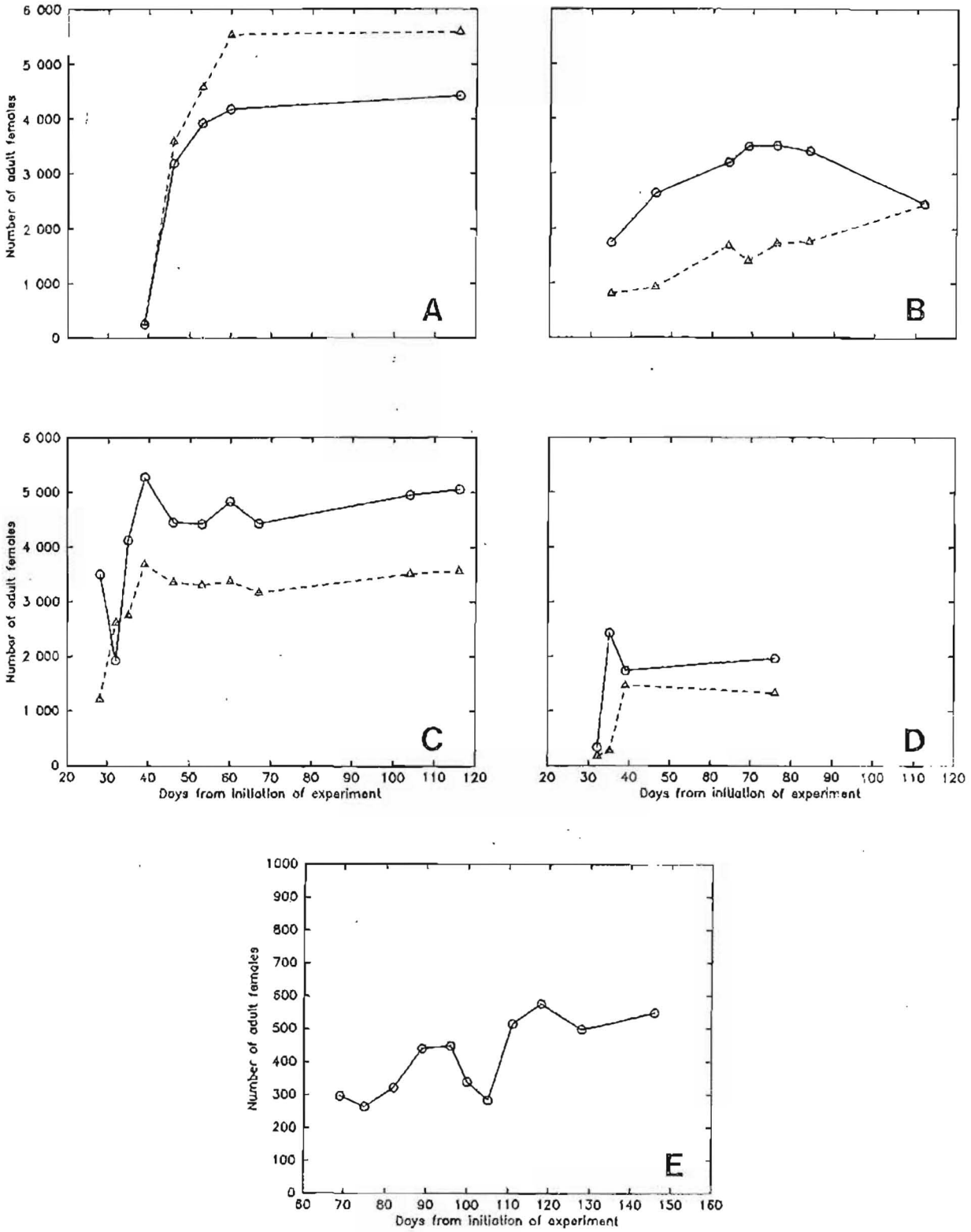
Values with letters in common did not differ significantly at the 5% level.

FIGURE 5.7

Frequency of adult females of G. rostochiensis and G. pallida at three sites and for two planting dates.

A = S4 early planting; B = S4 late planting; C = Cranford St.; early planting; D = Cranford St., late planting; E = Outram early planting.

circles with solid line = G. rostochiensis
triangles with short dashed line = G. pallida


Number of adult females
6 000
5 000
4 000
3 000
2 000
1 000
0
A
B
C
D
E
20 30 40 50 60 70 80 90 100 110 120
Days from initiation of experiment
1000
900
800
700
600
500
400
300
200
100
0
80 70 80 90 100 110 120 130 140 150 160

The increase in egg numbers per cyst (Figure 5.8) was slower in the early plantings than late plantings at S4 and Cranford St. but the final number of eggs produced was significantly higher ($P<0.05$) for the early plantings.

At Outram, the rate of increase of egg numbers was similar to that in Canterbury for early plantings; i.e. and it took approximately 80 days compared to 30-40 days for late plantings. However, the final mean number of eggs per cyst was 158 compared with an average of 198 eggs/cyst for the other Ro populations.

5.3.6 Life tables

Life tables were constructed for both Ro_4 and Pa_3 in two soil types and at two planting dates. Outram's early harvesting practices were examined and the effect on the mortality pattern of early and full maturity of the crop was examined.

Complete life tables for all experiments are presented in Table 5.8. Estimated numbers of larvae entering and leaving each life style provided a measure of mortality (100 qx) which was calculated according to Seber (1973) and was included in the life table computer program.

5.3.7 Life style mortality

Mortality values for each life style, for both species in two soil types and for two planting dates are examined separately below to simplify comparisons and highlight differences. The Outram population is not included in this comparison as Pa was not present there.

Mortality values were not obtained in replicate samples because the logistics of experimental procedures required for replication were beyond the capacity of this study. Statistical analysis of mortality values obtained for each life style therefore could not be carried out. Methods for calculation of variance for such life table estimates are not well established (Manly, 1977). The calculations are complex and require considerable access to computer time. However, to facilitate comparison of the variables (Ro v. Pa, silt v. peat and early v. late planting), each variable was considered separately by calculating the mean value of four data points so that three pairs of mean values could be compared (Table 5.9). The variable showing the greatest difference in paired comparisons was considered to have had the greatest influence on the mortality of that life style.

FIGURE 5.8

Fecundity (eggs/cyst) of G. rostochiensis and G. pallida at three sites and for two planting dates.

A = S4 early planting; B = S4 late planting; C = Cranford St., early planting; D = Cranford St., late planting; E = Outram early planting.

circles with solid line = G. rostochiensis
triangles with short dashed line = G. pallida

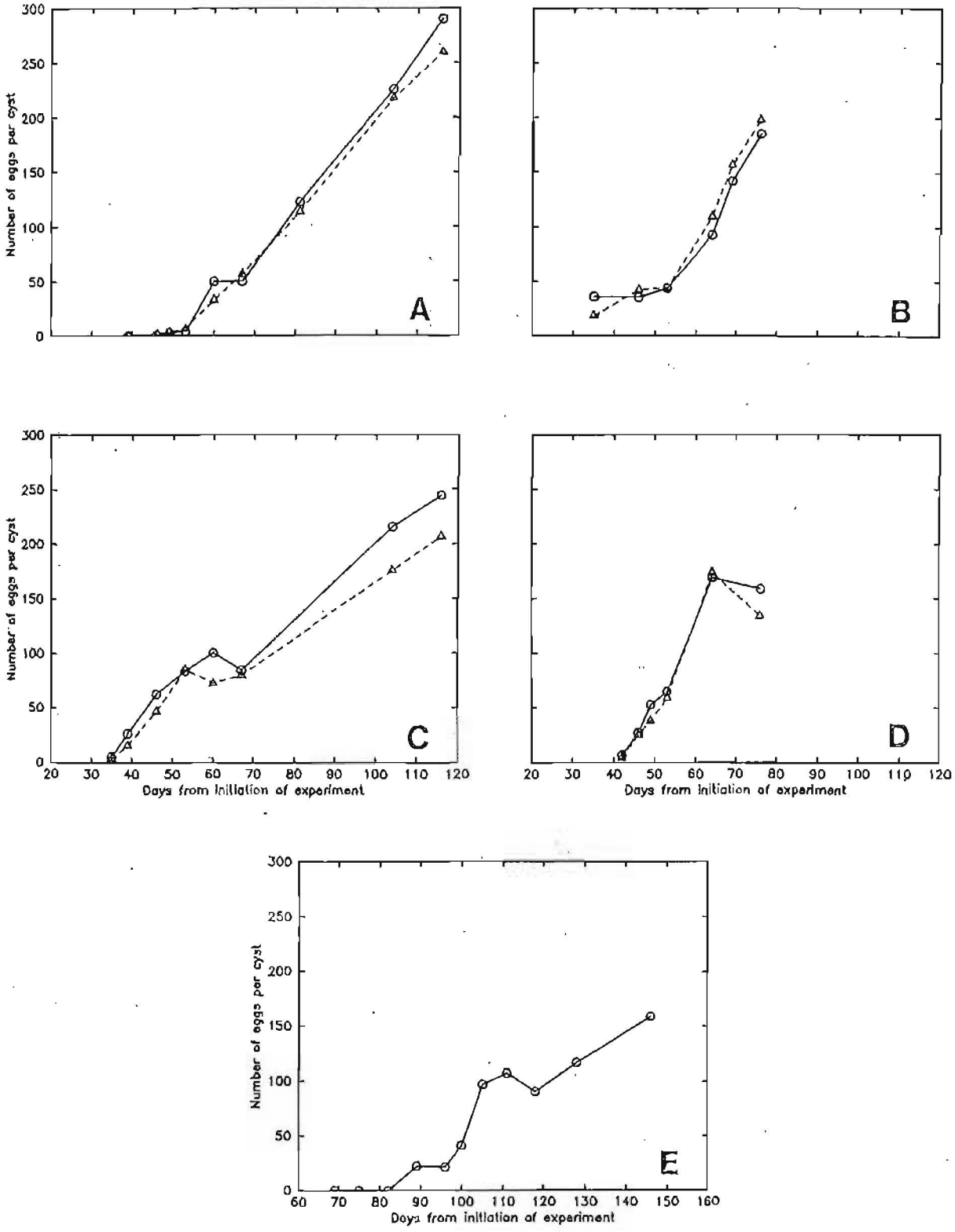

Number of eggs per cyst
Days from initiation of experiment
A
B
C
D
E

TABLE 5.8

Life tables for Ro and Pa in early and late planted potatoes grown in two soil types (S4 and Cranford St.). The number of individuals entering (and leaving) each style, and the average duration of the stage and calculated mortality are listed for each life style.

Entry phases:- 1, initial effective cohort; 2, second stage larvae entering the soil; 3, second stage larvae entering the root; 4, fourth stage juveniles (sub-adults); 5, breeding adults.

Life styles:- A, within cyst. B, within soil. C, within root feeding juveniles. D, adulthood.

TABLE 5.8

Ro Early plant slits

Entry phase	Life style	Mean duration (Days)	Number entering (1x)	Mortality % (100qx)
1			18347.2	
	A	20.0		13.6
2			15845.8	
	B	7.1		15.2
3			9272.8	
	C	14.0		53.4
4			5982.7	
	D	26.3		0.0
5			8912.4	

Ro Late planting slits

Entry phase	Life style	Mean duration (Days)	Number entering (1x)	Mortality % (100qx)
1			18454.0	
	A	17.0		0.0
2			18986.4	
	B	2.6		56.7
3			8219.2	
	C	9.9		8.5
4			7518.4	
	D	17.8		21.3
5			5920.5	

TABLE 5.8 cont.

Pa Early plant silts				
Entry phase	Life style	Mean duration (Days)	Number entering (1x)	Mortality % (100qx)
1			18918.2	
	A	25.0		9.2
2			17185.9	
	B	10.0		45.3
3			11041.1	
	C	20.7		6.2
4			10110.9	
	D	26.7		0.9
5			8734.6	

Pa Late planting silts				
Entry phase	Life style	Mean duration (Days)	Number entering (1x)	Mortality % (100qx)
1			17932.8	
	A	19.0		4.0
2			17211.7	
	B	3.6		79.5
3			3532.8	
	C	9.7		12.6
4			3087.3	
	D	14.8		0.0
5			3184.9	

TABLE 5.8 cont.

Ro Early planting peats

Entry phase	Life style	Mean duration (Days)	Number entering (lx)	Mortality % (100qx)
1			16680.3	
	A	11.0		6.2
2			15645.9	
	B	2.5		22.0
3			12197.4	
	C	6.9		19.4
4			9828.3	
	D	12.2		23.9
5			7481.8	

Ro Late planting peats

Entry phase	Life style	Mean duration (Days)	Number entering (lx)	Mortality % (100qx)
1			18531.7	
	A	23.0		0.0
2			18929.3	
	B	3.4		70.9
3			5509.9	
	C	7.2		31.6
4			3767.0	
	D	14.3		00.0
5			4312.1	

TABLE 5.8 cont.

Pa Early planting peats

Entry phase	Life style	Mean duration (Days)	Number entering (1x)	Mortality % (100qx)
1			19152.9	
	A	17.0		6.6
2			17881.6	
	B	5.6		61.2
3			6945.7	
	C	12.8		5.5
4			6561.1	
	D	21.8		26.1
5			4846.7	

Pa Late planting peats

Entry phase	Life style	Mean duration (Days)	Number entering (1x)	Mortality % (100qx)
1			18769.9	
	A	14.0		1.6
2			18474.2	
	B	5.4		83.8
3			2987.2	
	C	16.1		4.0
4			2868.8	
	D	27.6		30.9
5			1982.1	

TABLE 5.8 cont.

Ro Outram 100 days. (Duration curtailed by harvest)

Entry phase	Life style	Mean duration (Days)	Number entering (1x)	Mortality % (100qx)
1			7149	
	A	10.0		0.0
2			7734	
	B	21.4		81.1
3			1462	
	C	49.8		2.7
4			1422	
	D	127.8		51.3
5			692.6	

Ro Outram 150 days

Entry phase	Life style	Mean duration (Days)	Number entering (1x)	Mortality % (100qx)
1			7237.6	
	A	10.0		0.0
2			7807.2	
	B	21.5		81.3
3			1456.3	
	C	50.2		2.7
4			1416.3	
	D	132.9		37.9
5			879.3	

Mortality in life style A (within the cyst)

Percentage mortality in life style A (Table 5.9) was low compared to other life styles under all experimental conditions (8.9 early v. 1.4 late). Early planting dates exposed populations to greater mortality. Soil type also influenced mortality, its effect was lowest in peat soils (3.6 peat v. 6.7 silts).

Mortality in life style B (within soil active L_2 stage)

Life style B had the highest mortality of all life styles (Table 5.9). Planting date again had the greatest influence, late planting caused the highest mortality. Pa had a higher mortality than Ro under all environmental conditions.

Mortality in life style C (within root feeding juveniles L_2 and L_3)

Mortality in life style C (Table 5.9) was generally lower than for style B, and in all but one condition (late planting silt) was higher in Ro than Pa. Higher mortality was observed in early plantings and in silt soils.

TABLE 5.9

Percentage mortality in each life style for both Ro and Pa in two soil types and for two planting dates.

Environmental condition	A Life style Species Ro	Pa	Planting date mean	B Life style Species Ro	Pa	Planting date mean
Early planting silt	13.6	9.2		15.2	45.3	
			8.9			35.9
Early planting peat	6.2	6.6		22.0	61.2	
Late planting silt	0.	4.0		56.7	79.5	
			1.4			72.7
Late planting peat	0	1.6		70.9	83.8	
Species mean	4.9	5.3		41.1	67.4	
Soil type : silt	6.7			49.2		
mean : peat	3.6			59.5		

Environmental condition	C Life style Species Ro	Pa	Planting date mean	D Life style Species Ro	Pa	Planting date mean
Early planting silt	53.4	6.2		0.0	0.9	
			21.1			12.7
Early planting peat	19.4	5.5		23.9	26.1	
Late planting silt	8.5	12.6		21.3	0.0	
			14.2			13.0
Late planting peat	31.6	4.0		0.0	30.9	
Species mean	28.2	7.1		11.3	17.6	
Soil type : silt	20.2			5.6		
mean : peat	15.1			20.2		

Mortality in life style D (adulthood)

The level of mortality in this style was variable and the presence of several zero values rendered comparisons meaningless.

Life style mortality in the Outram population

Life style mortality in the Outram population is shown in Table 5.10.

TABLE 5.10

Percent mortality of all life styles in the Outram population at two harvesting dates.

	Life styles				
	A	B	C	D 100 days	D 150 days
Per cent mortality	0.0	81.8	2.7	51.3	37.9

The pattern of mortality was similar to that observed in the Canterbury populations. Low mortality occurred in the cyst stage (style A) and high mortality in the soil phase (style B). Life style C occurs within the root and its mortality was much lower than in the Ro populations examined in Canterbury. On the other hand, mortality of adults (style D) was higher than in comparable Canterbury populations. The effect of premature removal of the host plant (harvesting after 100 days) was marked and mortality in the adult stage (life style D) increased from 37.9% to 51.3%.

5.3.8 Duration of life styles

Duration of life styles is shown in Table 5.11. To facilitate comparisons between species, soil type and mean planting date values have been calculated as described in Section 5.3.7.

The most consistent feature observed is that mean duration of Ro was shorter than that of Pa for all life styles.

The duration of life style A (within the cyst) was greater in the peat soils than in the silts and under all conditions was slightly

shorter in Ro.

Life style B (within soil) was the briefest of all life styles and in all but one instance (Ro in peat) its duration was shorter in late plantings than early plantings.

The duration of life style C (in root) was shorter in Ro than in Pa and neither planting date nor soil type had much influence on its duration. The duration of life style D was generally shorter in Ro than Pa (Table 5.11). The influences of planting date and soil type were small.

5.3.9 Overall life cycle duration

The duration of life cycles (sum of all life styles) is shown in Table 5.12. Under almost all conditions Ro had a shorter life cycle than Pa. The exception was late planting in silt where life cycle durations were very similar. Mean values for planting dates and soil types indicated that duration of life cycles tended to be shorter under late plantings (48.8 v. 60.4 days) and in peat soils (47.7 v. 61.5 days).

TABLE 5.12

Duration of life cycles of both species in different environmental conditions.

Experimental situation	Duration (days) Ro	Pa	mean
Early planting silt	67.4	84.3	
			60.4
Early planting peat	32.6	57.2	
Late planting silt	47.3	47.1	
			48.8
Late planting peat	37.9	63.1	
Species mean	46.3	62.9	
Soil type: silt		61.5	
mean : peat		47.7	

5.3.10 Influence of physical factors on the life cycle of potato cyst nematodes

Soil temperature and moisture are the physical factors that have the greatest direct effect on growth and development of the nematode and its host (Jones, 1975). The effect of soil type was examined indirectly by simultaneously conducting identical experiments in both silt and peat soils.

The influence of soil temperature and moisture was examined in detail during the course of the experiments and mean values for each life style were calculated.

Soil temperature

The mean soil temperature to which each life style was exposed is shown in Table 5.13. In Canterbury, temperatures remained stable in all situations except early plantings on silt soils where they increased slightly as each successive life style appeared. Temperatures in peat were consistently higher than in silt.

At Outram, the range of temperatures that each life style was exposed to was much greater; the maximum difference being 11.6^{o}C between styles A and D. This was a consequence of the very early planting date.

Mortality of eggs and larvae in life style A was related inversely to temperature (Figure 5.9A, Table 5.13). No significant differences in mortality at different temperatures were found between the two species. Mortality in life style B was greater at higher temperatures (Figure 5.9B) in both Ro and Pa. However, within the same range of temperatures Pa had a higher mortality than Ro.

The population at Outram behaved differently in that mortality/temperature values for life styles A and B were totally dissimilar to those encountered in Canterbury (Table 5.9, Table 5.13).

Fecundity (eggs/cyst) (Figure 5.9C) showed a negative relationship with soil temperature and again there was no difference between species.

FIGURE 5.9

The relationship between soil temperature and percent mortality in life styles A and B and the fecundity of adult females of *G. rostochiensis* and *G. pallida*.

A = mortality of life style A Ro
B = mortality of life style A Pa
C = mortality of life style B Ro
D = mortality of life style B Pa
E = fecundity of adult females Ro
F = fecundity of adult females Pa

circles = *G. rostochiensis*
triangles = *G. pallida*
solid line = fitted regression line Ro
short dashed line = fitted regression line Pa

Straight line fitted by least squares line of best fit.

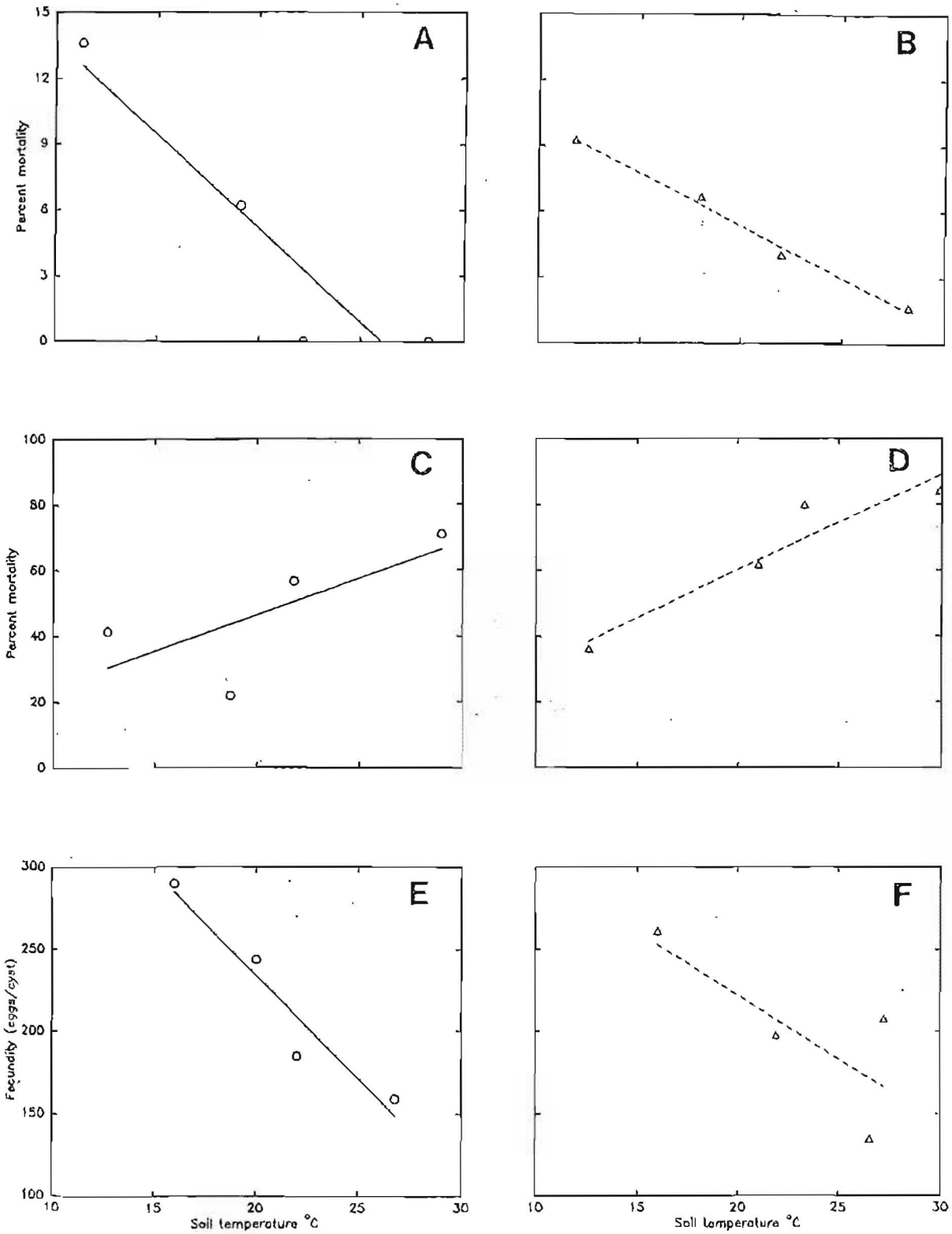

A
B
C
D
E
F
Percent mortality
Percent mortality
Fecundity (eggs/cyst)
Soil temperature °C
Soil temperature °C
0
3
6
9
12
15
0
20
40
60
80
100
100
150
200
250
300
10
15
20
25
30

TABLE 5.13

Mean soil temperatures (°C) to which each life style was exposed in different experiments.

Experimental situation	Life styles A	B	C	D	Life cycle mean	Planting date mean
Ro Early planting silt	11.3	12.7	14.7	16.1	13.7	
						13.8
Pa Early planting silt	11.8	12.6	15.9	16.0	14.0	
Ro Late planting silt	22.2	21.8	22.9	22.0	22.0	
						22.3
Pa Late planting silt	22.0	23.3	22.4	21.9	22.4	
Ro Early planting peat	19.1	18.7	17.6	20.8	19.0	
						19.8
Pa Early planting peat	18.7	21.0	21.5	21.2	20.6	
Ro Late planting peat	28.3	29.0	28.1	26.8	28.0	
						27.7
Pa Late planting peat	28.2	29.9	25.0	26.5	27.4	
Ro Early planting Outram	9.4	15.1	17.0	21.0	15.6	15.6

Soil moisture

Mean soil moisture encountered by each life style of both species in the different environments is presented in Table 5.14. In all experiments water was applied to prevent plants wilting.

TABLE 5.14

Mean soil moisture as percent oven dry weight for each life style of both species in different environmental conditions.

Experimental situation	Life styles A	B	C	D	Life cycle mean	Planting date mean
Ro early planting silt	25.1	23.6	23.9	18.5	22.7	
						22.3
Pa early planting silt	24.9	22.8	23.5	17.0	22.0	
Ro late planting silt	22.6	18.4	14.6	21.9	19.3	
						18.5
Pa late planting silt	21.5	16.5	14.6	18.2	17.7	
Ro early planting peat	85.4	84.7	90.2	59.0	79.8	
						75.0
Pa early planting peat	78.5	103.0	49.1	50.4	70.2	
Ro late planting peat	43.7	47.6	49.5	62.3	50.7	
						53.3
Pa late planting peat	43.7	47.6	58.0	74.8	56.0	
Ro early harvest Outram	22.2	30.5	26.7	23.1	25.6	
						25.3
Ro late harvest Outram	22.2	30.5	26.7	22.4	25.1	

There was a marked difference in moisture content of silt and peat soils

but because only a few data points were available for each soil type the effects of different moisture regimes on the nematode populations are difficult to interpret and few trends were apparent. Thus, in Canterbury, mortality in life style B (Table 5.9) was lower under higher soil moisture conditions for both silt and peat, but at Outram mortality was very high (81%) at an above average soil moisture level of 30.5% oven dry weight.

5.3.11 Survival curves

Survival curves describing the number of individuals entering each life style are shown in Figure 5.10.

Survival curves displayed a basic sigmoid shape produced as a result of high mortality in life style B and lower mortality in life styles A, C and D.

Overall survivorship was lower for Pa than Ro in each environment. Mean survivorship for Ro in all situations was 37% whereas that for Pa was 24%. Survival tended to be higher in early plantings than late plantings in the Canterbury region.

5.3.12 Key mortality factors

The ultimate aim of life table analysis is to identify stages within life cycles which are most vulnerable to change and which therefore have most effect on final suvivorship. The method of key factor analysis described by Varley and Gradwell (1960) was used to determine which of the four life styles had most influence on overall mortality. Mortalities of each style (logarithmically transformed; Appendix XVII) are compared graphically with overall mortality. Results are presented in Figure 5.11.

The slope of curve k_B (mortality of life style B, mimics that of K (total mortality) which indicates that larvae moving through the soil are the most vulnerable part of the life cycle.

5.3.13 Multiplication rate

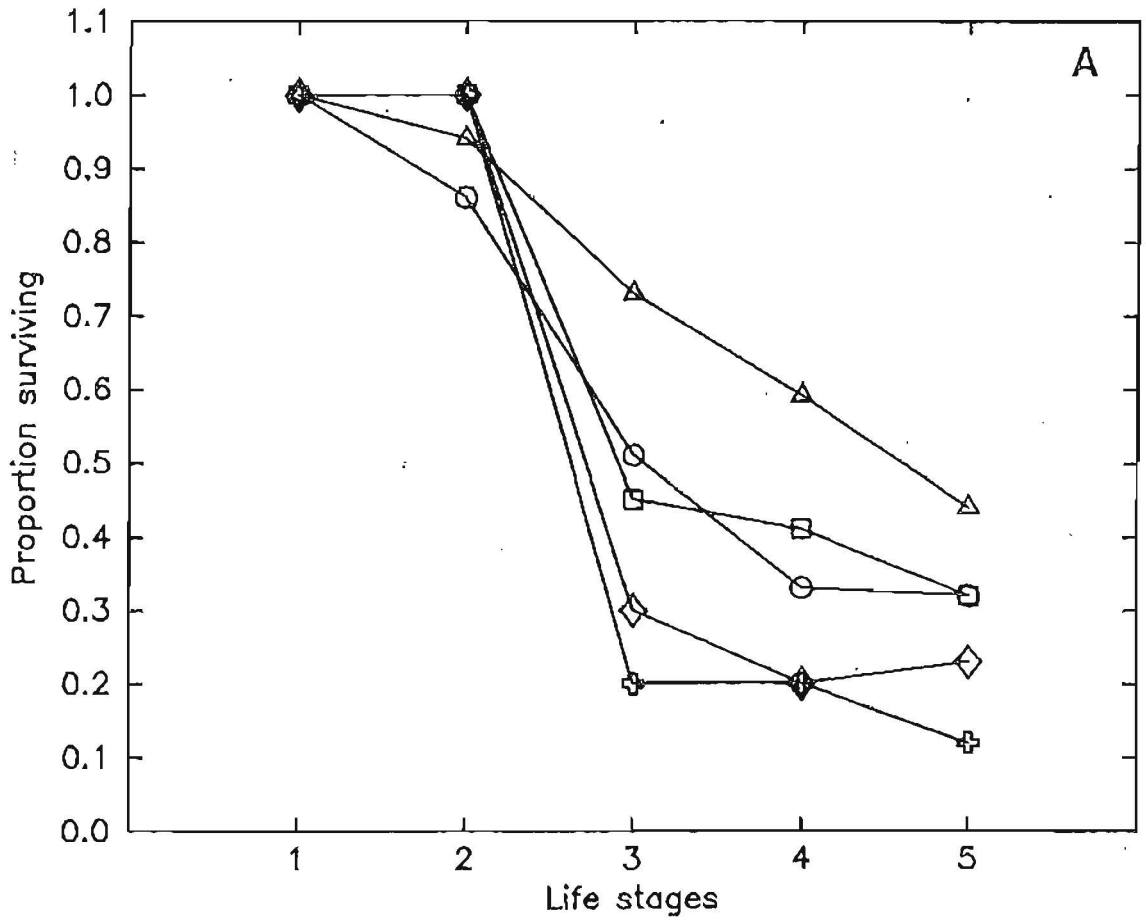
Although high mortality in life style B and to a lesser extent the other life styles played a significant part in determining the final number of individuals that survived to reproduce, the environment in which females (style D) developed had an important influence on fecundity, measured as numbers of eggs per cyst. The measure of success in any life style is the level of increase or multiplication achieved. In the case of the cyst nematode only a proportion of the eggs within a cyst have the potential to hatch and develop (the effective inoculum) and

FIGURE 5.10

Survival curves for *G. rostochiensis* and *G. pallida* at three sites and for two planting dates.

A = survival curves for *G. rostochiensis*
B = survival curves for *G. pallida*

circles = S4 early planting
squares = S4 late planting
triangles = Cranford St. early planting
diamonds = Cranford St., late planting
swiss cross = Outram early planting


A
Proportion surviving
1.1
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
1
2
3
4
5
Life stages

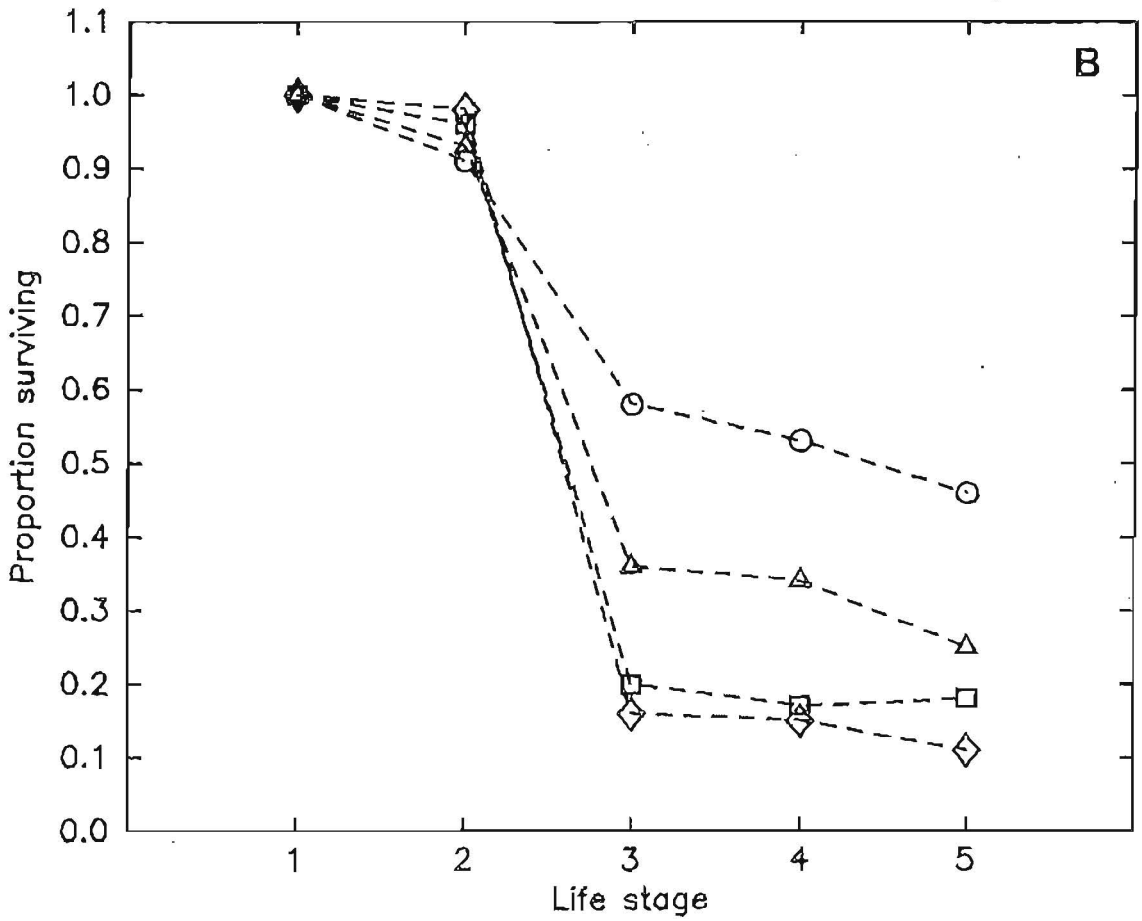
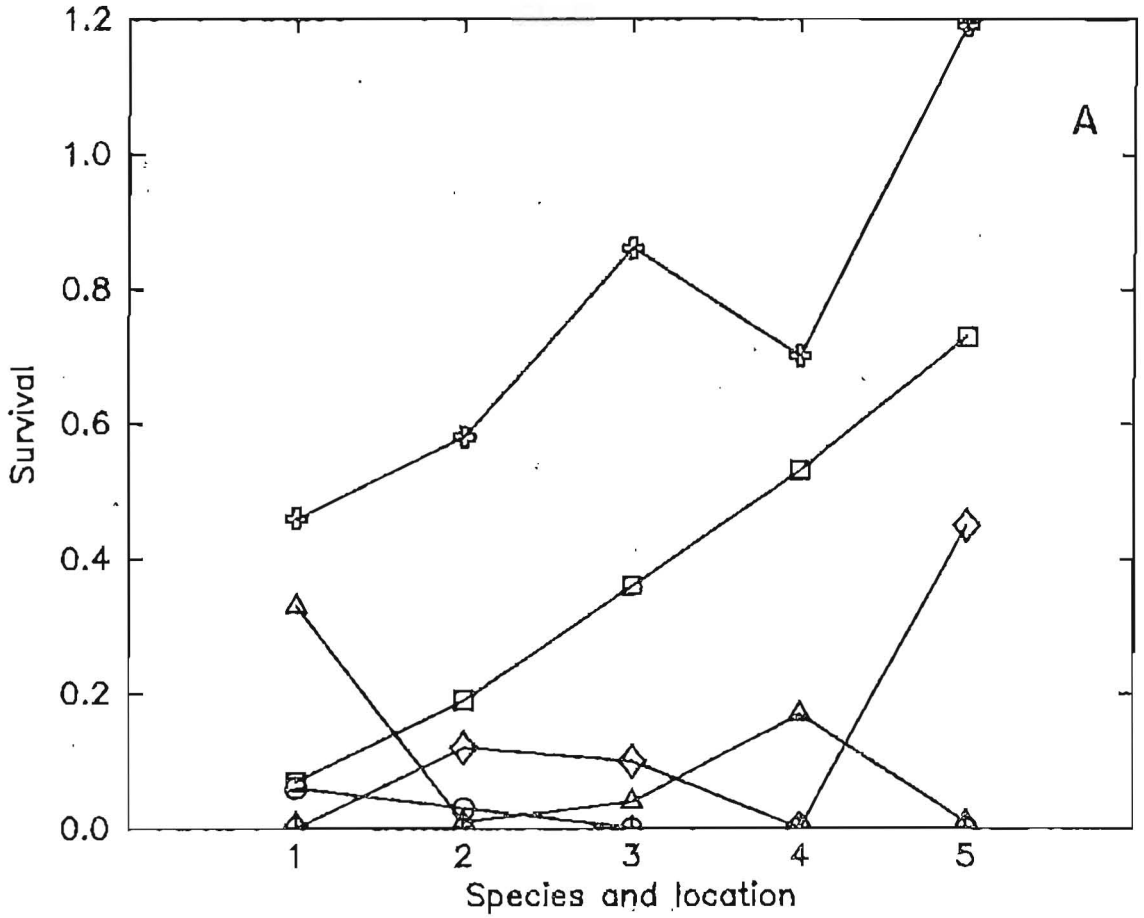

B
Proportion surviving
1.1
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
1
2
3
4
5
Life stage

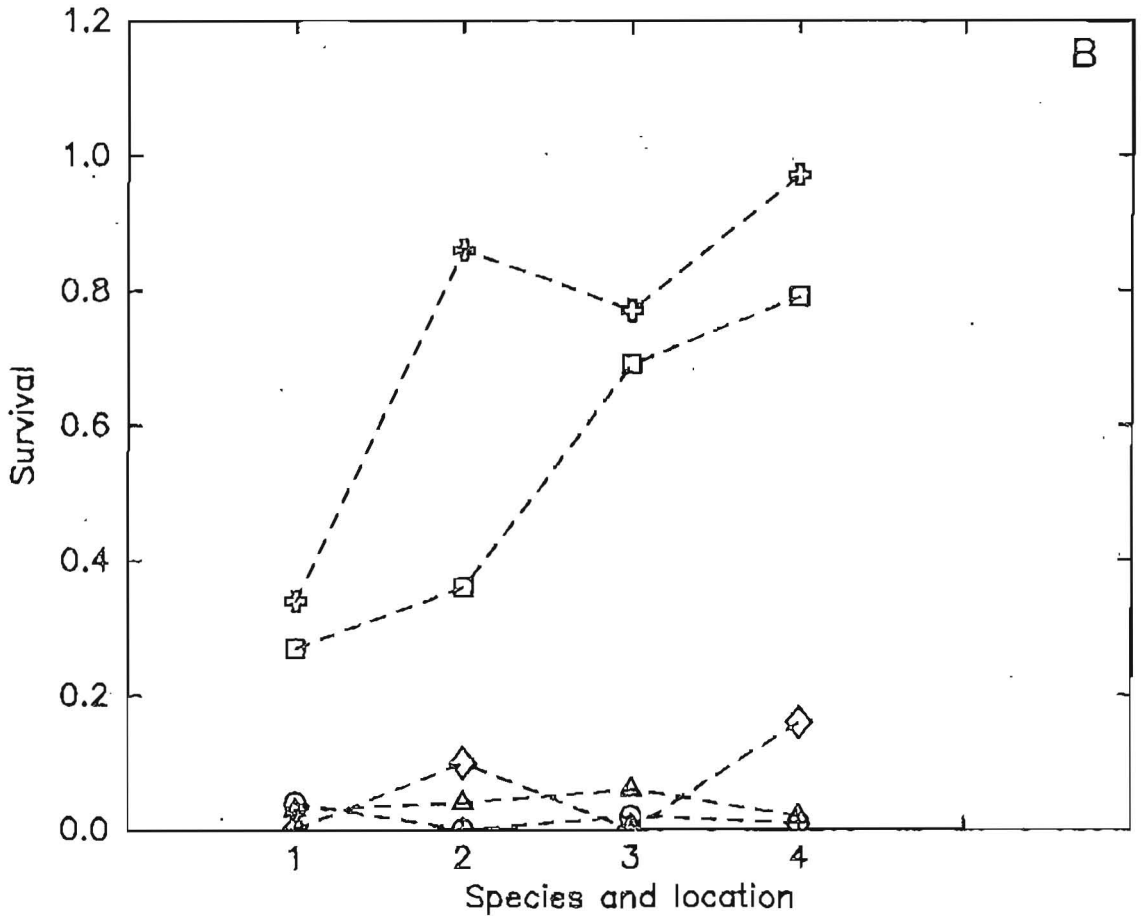
FIGURE 5.11

Graphical key factor analysis of mortalities in the four life styles at three sites and for two planting dates for G. rostochiensis and G. pallida.

1 = S4 early planting
2 = Cranford St.. early planting
3 = S4 late planting
4 = Cranford St.. late planting
5 = Outram early planting late harvest

circles = k_A life style A
squares = k_B life style B
triangles = k_C life style C
diamonds = k_D life style D
swiss cross = k total mortality


A
Survival
1.2
1.0
0.8
0.6
0.4
0.2
0.0
1
2
3
4
5
Species and location


B
Survival
1.2
1.0
0.8
0.6
0.4
0.2
0.0
1
2
3
4
Species and location

similarly, only a proportion of the eggs produced by developing females are alive (Table 5.15).

TABLE 5.15

The proportion of live eggs produced by adult females at the completion of life style D under different environmental conditions.

Soil type/planting date	Species	
	Ro	Pa
Early planting silt	0.92	0.94
Late planting silt	0.91	0.88
Early planting peat	0.89	0.88
Late planting peat	0.92	0.93
Early harvest Outram	0.55	-
Late harvest Outram	0.85	-

To estimate the effective multiplication at the end of the life cycle, the number of live eggs produced by the new generation was divided by the number of effective eggs in the initial inoculum. Results of these calculations are shown in Table 5.16.

Multiplication rates varied widely and were influenced strongly by planting date. Significant differences ($p<0.05$) between populations in early and late plantings were observed for both soil types. Generally, Ro had a higher multiplication rate than Pa, but it was significantly different ($p<0.05$) only in the peat. Multiplication rates at Outram differed between the two harvesting dates as a result of differences in both the total number of adult females produced and their fecundity. The practice of early harvesting reduced numbers of cysts and eggs.

TABLE 5.16

Effective multiplication rates of both species under different environmental conditions.

Soil type/planting date	Species	
	Ro	Pa
Early planting silt	41.2 a	51.8 a
Late planting silt	18.4 bc	14.6 c
Early planting peat	39.2 a	24.6 b
Late planting peat	11.6 c	7.1 d
Early Harvest Outram	0.4 e	-
Late Harvest Outram	3.0 d	-

Values with letters in common are not significantly different at the 5% level.

5.4 DISCUSSION

Life table analysis was an ideal technique for making detailed comparisons between Ro and Pa living under the same and different environmental conditions. A comparison of the two soil types in Canterbury formed the core of the work and the Outram population was included because of the unique cropping pattern employed there.

Egg hatching within the cyst occurred in Canterbury shortly after the host potato had been planted and in all cases Ro hatched more quickly than Pa regardless of environmental conditions. Mean hatching time did not differ significantly between species but there was a consistent trend for earlier hatching in populations that developed in these late plantings. They were subjected to higher soil temperatures and lower soil moisture. The time taken for root initiation in the early and late plantings did not differ significantly and in all cases, except for Outram, root production was measurable within seven days.

TABLE 5.17

Days between planting of host potatoes and detection of measurable and maximum root weight for two planting dates and three locations (n=4).

	First measurable root weight		Maximum root weight	
Planting date and soil type	mean day	weight (g) mean (±SE)	mean day	weight (g) mean (±SE)
Early planting silt	7	0.3(± 0.07)	49	28.9(± 3.91)
Late planting silt	4	0.2(± 0.07)	55	20.5(± 2.77)
Early planting peat	4	0.2(± 0.05)	40	28.5(± 2.43)
Late planting peat	4	0.5(± 0.09)	23	21.8(± 1.40)
Early planting Outram	14	0.5(± 0.04)	96	19.6(± 0.62)

On the other hand, the maximum weight of root produced per plant was lower in later planted crops at all locations (Table 5.17). Nevertheless, it appeared that the plants were still sufficiently vigorous to sustain developing nematode populations. Premature root death was not evident in any of the experiments and this also suggested that levels of nematode hatch and establishment in the hosts were in response to prevailing environmental factors rather than the status of the plant. The proportion of eggs that finally hatched from a cyst was high and although a higher proportion hatched from Pa the differences were not statistically significant.

Mortality within cysts was always low and showed a slight but non-significant rise over the course of the experiments. Ro was capable of responding more rapidly to stimulation or perhaps to lower levels of

stimulation from the host root. In a competitive situation this should give it a distinct advantage over the other species by enabling it to select the best feeding sites on the root.

Larval development was generally slower in Pa than Ro, and this appeared to be the case throughout the entire life cycle. The difference between the two species was more obvious in early plantings.

The frequency curves for L_2 larvae within roots tended to have a flattened profile with extended tails. By comparison curves for L_3 and L_4 larvae had well defined peaks with relatively short tails (Figures 5.3, 5.4, 5.5). The frequency curves for the Outram nematode population were particularly extended apparently in response to some indirect environmental effect related to slower host development.

L_4 larvae occurred either concurrently with, or seven to eleven days before tuber initiation regardless of location, species or planting date (Table 5.18).

At this time the plant is in the process of tuber formation and the nematode feeding diverts metabolites for their own development. A heavy feeding demand before this time would seriously weaken both the plant and consequently endanger the parasite population.

TABLE 5.18

The interval in days between the presence of L_4 larvae and the initiation of tuber forming stolons on the host plant.

	species	
Experimental situation	Ro days	Pa days
Early planting silt	7	7
Early planting peat	11	7
Late planting silt	7	7
Late planting peat	0	0
Early planting Outram	8	-

Overall sex ratios (Sr_{tot}) of L_4 larvae within each species did not differ between experiments but in Pa slightly more nematodes were female than in Ro. Ro hatches more quickly and develops more rapidly in the root than Pa and this suggests that Ro puts pressure on the host. In the Canterbury silt and peat soil experiments, a mean of 9,840 Ro L_2 larvae established in each plant, but the mean was only 5,714 per plant for Pa.

Once established in feeding sites nematodes begin to grow, and according to Trudgill (1967), females develop from larvae occupying the best sites. Mugniery and Fayet (1981) showed that more females developed in larger diameter roots than small ones, and in a developing root structure the primary roots are thicker than secondary roots. During my experiments a larger number of Ro than Pa larvae established in the roots and there may have been some intraspecific competition for feeding sites at the level of inoculum used. As a result, some larvae probably established on secondary roots. A lower proportion of females would be expected under such circumstances. In contrast, Pa with its higher L_2 mortality in the soil could be expected to show less intraspecific competition for primary root sites and therefore a higher proportion of females should develop.

The life tables showed that mortality and duration of the four life styles varied between species and within species depending on environmental conditions. Mortality within the cyst (life style A) was low in both species under all environmental conditions tested and showed that changes within the cyst occurred principally as a result of active egg hatching and emigration. Mortality in life style A was higher in early than late plantings as a result of lower soil temperatures; higher mortality occurred in peat soils. The duration of life style A was longer in peat than silt, possibly as a result of slower diffusion of root exudates through the highly organic peat soil. Highest mortality occurred in life style B (within soil). This emphasises the hazards associated with the free living phase in the soil and finding the host. Higher soil temperatures associated with late plantings increased the mortality of life style B. Ro had lower mortality and shorter duration in life style B than Pa under all conditions. The shorter period in the hazardous soil environment was probably responsible for the lower mortality in Ro. Plantings at Outram were made at a lower soil

temperature (9.4°C) than in Canterbury and mortality was higher. This suggests that the population at Outram may be living near the lower end of the temperature range suitable for Ro (Foot, 1978b). Since similar soil moisture levels in silt (S4) and silt/loam (Outram) were associated with widely different mortalities in life style B (early plantings) it seems unlikely that soil moisture levels directly influence mortality. Mean mortality of life style C (within root) was much lower than in style B in all experiments (18% compared to 55%) and probably reflects the insulatory effect of root tissue. Once within the host root, sources of mortality present in life style B are no longer of much consequence.

Instead, environmental influences will be expressed indirectly through changes in the host's physiology. Although mortality in life style C was not as high as in life style B it was higher in Ro than Pa in plants grown in the same environment (Table 5.8). The duration of this life style was also shorter in Ro than Pa. I consider that the higher mortality in Ro is one expression of intraspecific competition associated with its greater numbers and more rapid development. Such competition probably occurs first when large numbers of L_2 larvae attempt to penetrate the host and may be intensified by the high degree of hatching synchrony in Ro and the brief soil phase at a time when host development is limited. These factors do not necessarily result in increased larval mortality (Jones and Kempton, 1978) but a greater proportion of the larvae are forced into less favourable feeding sites, and thus are disposed towards maleness (Trudgill, 1967). Mugniery and Fayet (1981) also noted that with increasing density, competition for feeding sites has an adverse effect on the developing female. The behaviour of the Outram population conforms to this kind of pattern. Lower numbers of L_2 larvae invaded the roots over a longer period and thus were able to select more suitable sites. The combination of low numbers and an extended establishment period resulted in low mortality and a high proportion of female L_4 larvae.

Measurement of mortality in adult females (life style D) was not satisfactory, but the number of eggs per cyst (fecundity), the end result of female development, was strongly influenced by planting date. Fecundity was higher in early plantings than late plantings in both species.

In Canterbury (silts and peats), the newly developed cyst contained few dead eggs (9% overall) but at Outram the proportion was much higher. Under late harvest conditions the proportion of dead eggs was 15% but under early harvest conditions it was 45%. A pecularity of early harvest cysts was that immediate assessment of viability on the

newly produced eggs (using Meldola's method) indicated that all were dead, but when stored under field conditions for 50 days and then reassessed, 55% of the eggs were found to be viable. The significance of this finding is that a proportion of eggs can continue to develop in a cyst which is prematurely deprived of its host.

Final multiplication values which take into account the number of cysts produced and their fecundity show that in all experimental conditions except in the early planting at S4, Ro had a higher multiplication rate than Pa. In Ro this is the result of greater survival of L_2 larvae and as a consequence the production of a higher number of cysts at the end of the life cycle. Pa on the other hand had greater larval mortality despite a sex ratio that slightly favoured more females and fewer cysts were produced. Pa in the early planting at S4 had a lower life style B mortality, but an increase in the number of females gave a higher multiplication rate in Pa than in Ro. The lower soil temperatures encountered at this planting date favoured Pa over Ro. The main difference in the population biology of Ro and Pa appears to be the relative degree of larval mortality under various conditions particularly in life style B. The shorter duration of the Ro population in this life style is largely responsible. Multiplication values produced from the Ro population at Outram were lower than in Canterbury as a result of higher mortality of L_2 larvae and lower production of viable eggs. The practice of early harvesting at Outram also reduced numbers of cysts.

5.5 CONCLUSION

Two main sets of interacting influences affected the active part of the potato cyst nematode life cycle and resulted in differences in the rates of mortality and multiplication under similar inoculum loads.

They are:-

(1) Species differences which appear as developmental and behavioural responses in each life style.

(2) Environmental factors such as soil temperature, soil moisture and host plant vigour. Changes in these factors may modify the success of both species or favour one over the other.

Species differences and observed environmental factors that influence the success of the two species are presented in the summary.

5.6 SUMMARY

Summary of species differences and the influence of environmental effects on the development of potato cyst nematodes in the South Island.

Life style	Species differences	Environmental influences
A (In cyst)	Ro has shorter duration	Mortality reduced with increasing soil temperatures.
B (In soil)	Ro hatches earlier Ro has lower mortality and shorter duration	Increased mortality at high soil temperature and low soil moisture. Duration is reduced at higher temperature.
C (In root)	Ro has higher mortality Ro has more males Ro has shorter duration	Larval development is synchronised with host development. Environmental influences are reduced by the insulating effect of host tissue.
D (Adulthood)	Pa is slower to complete life cycle.	Higher temperatures result in lower fecundity. Host status influences egg development.

CHAPTER 6

SPECIES INTERACTION ON THE SAME HOST

6.1 INTRODUCTION

Both species of potato cyst nematode have been found as mixed populations in most European countries (Parrott and Berry, 1978; Oydvin, 1978; Magnusson, 1979; Kort and Bakker, 1980). Canto Saenz and Mayer De Scurrah (1977) found mixtures of Pa and Ro in relatively undisturbed populations in South America. The effects of competition between the two species were observed in the field by Cole and Howard (1962) and Huijsman (1961). They found that a very low (initially undetectable) level of Pa could co-exist in a field of predominantly Ro but would not increase until the population dominance of Ro had been reduced by the use of Ro resistant potato cultivars. Jones and Perry (1978) used the data of the above workers to construct a model of competition between Ro and Pa. However, from experimental evidence it is unclear which species is dominant as no consistent response has been observed. McKenna and Winslow (1972) and Parrott et al. (1975) found that Pa was dominant but Parrott and Berry (1978) found that Ro was dominant. The observations of Cole and Howard (1962) and Huijsman (1961) support the dominant status of Ro.

In the South Island of New Zealand, mixed populations of Ro and Pa have been found (Nicol, 1977) but no information has been obtained on the relative abundance of the two species. A knowledge of species interactions is important for the long term management of the pest in Canterbury and the presence of mixtures makes it highly likely that at least some apparently pure populations in the same area are in fact undetected mixtures (i.e. one species at very low density). If this is so, a management strategy is needed which will extend the useful life of Ro resistant potato cultivars until a cultivar with combined Ro and Pa resistance is available.

As part of my study I carried out experiments both in the field and in the glasshouse to examine interactions between the species and to determine which species is more successful.

6.2 EXPERIMENTAL DESIGN

Two different techniques were used in experiments 1 and 2.

Experiment 1

Single cohort/host units were established in double walled terylene bags. This technique is detailed in the Chapter 2.5.1. Because it was field based, the cohort/host units were subjected to normal environmental conditions which in turn influenced the performance of the two nematode species. Sachets containing the whole cyst inoculum were distributed through the soil.

Experiment 2

Single cohort/host units (600 ml plastic pots) were grown under controlled glasshouse conditions to minimise observed environmental effects on the two nematode species. Egg suspensions, rather than whole cysts, were used as inocula to minimise observed differences in hatching times between Ro and Pa. Both controlled environments and egg suspensions were used to produce unbiased interactions between the species and to provide a base line against which field populations could be compared.

In all experiments, both Ro_4 and Pa_3 were inoculated simultaneously on to a host plant. The proportions of the two species were set at the beginning of the experiment and at its completion the proportions of the two species as newly produced cysts were determined.

To avoid confounding effects of additivity, which results from changing the ratio of a mixture by altering the density of one component while keeping the other fixed, substitutive designs (Harper, 1977) were used. These allowed the relative proportions of the two species to alter, but ensured that total nematode density (eggs/ml) was held constant.

The substitutive experimental design used in this study was developed by De Wit (1960) and incorporated a "replacement series" of species ratio classes. The replacement series is shown in Table 6.1 and was used in both experiments 1 and 2. In addition, experiment 2 was expanded to include a range of densities for each replacement series.

TABLE 6.1

The proportions of Ro and Pa used in the replacement series experiments.

	Pa	100	99	90	50	10	1	0
Ratio classes	:	:	:	:	:	:	:	:
	Ro	0	1	10	50	90	99	100

6.3 METHODS

6.3.1 Experiment 1

For each ratio class the inoculum density was 10 eggs/ml. The cysts required to produce the appropriate densities for each ratio class were counted out by hand. Cysts used were selected from a single generation population which had been selected for evenness of size. After the correct number of cysts of each size had been counted out they were mixed together and subsequently divided into eight inoculum sachets.

For each ratio set four replicates were produced and each replicate was inoculated into 2.0 litres of clean field soil contained in the terylene bags. All treatments and replicates were labelled and planted in random order in a field plot. Host plants were allowed to grow to full maturity before harvesting.

6.3.2 Experiment 2

Host plants were grown in 600 ml of sterilised potting soil; free eggs rather than whole cysts were used, and the egg suspension was injected into the root zone of an actively growing plant.

Egg suspensions of both species were obtained by crushing whole cysts and releasing the eggs. The eggs were dispersed in aerated water and the final egg density was achieved by adjusting the volume of water. From this stock suspension the appropriate number of eggs was withdrawn to make up the ratio sets (Table 6.1).

For each ratio set a range of overall densities was made up from

the stock suspension. Densities selected were based on the only initial density/multiplication curve known for a New Zealand population (Foot pers. comm.) and are shown in Table 6.2

TABLE 6.2

Range of initial densities used for each replacement series experiment.

Initial densities (eggs/ml)			
0.3	2.4	19.2	153.0

Glasshouse conditions

Host plants were grown for approximately 30 days and had produced an even quantity of visible roots before the inoculum was injected into the root ball. Each host plant was injected at four equidistant points between the main stem and the sides of the plastic pot. Each treatment consisted of four plants inoculated in this way and placed randomly on a bench in a controlled temperature glasshouse. All 150 bags were blocked together and surrounded by a double row of buffer pots. Plants grew at a soil temperature of $17.5^{o} \pm 1^{o}C$ and were watered every day. All plants were allowed to reach maturity and die down before harvesting.

6.3.3 Identification of progeny

The gross morphology of mature cysts of the two species is very similar and cannot be used to distinguish between them. Measurement of L_2 larvae has been used to distinguish the species (Stone, 1972) but for critical identification extensive measurements are required. Even then, morphological variations within species can make this technique unsatisfactory. Selective resistance by a potato cultivar to one or other species of nematode is another method that has been used by Jones (1957) and Green *et al.* (1970) to differentiate Pa from Ro in mixed populations. This technique depends on the fact that *Solanum tuberosum* subsp. *andigena* CPC 1673 (Ellenby, 1954a) is resistant to Ro but not Pa. The presence of white cysts on the root ball of the CPC 1673 derived cultivar Maris Anchor indicates that Pa is present.

To determine changes in the relative proportions of progeny in each ratio class, 100 cysts were inoculated individually on to 100 Ro resistant Maris Anchor plants placed in polystyrene propagating trays. These commercially available trays are 50 mm thick and have rows of conical holes punched in them. There are 50 holes in a tray and each hole contains 50 ml of soil (Figure 6.1 A). Two trays with a total of 100 holes were used for each test. In the bottom of each hole a plastic wad was placed to retain moisture and roots (Figure 6.1 B). A sprouted 10 g tuber was placed on top of the wad and the 100 cysts to be tested were counted individually on to a damp 4 mm circle of filter paper (Figure 6.1 C). This was placed on the inside of each hole and covered with standard potting mix.

All trays were labelled, and placed in random order in a 50% light excluding shade house (Figure 2.1A) which kept the soil temperature between 15 and 22°C. Trays were watered daily.

The number of tubers that failed to grow was recorded to allow adjustments to be made to final root ball counts. After 60 days the root balls were examined and the number supporting white cysts determined. All cysts found were assumed to have developed from a single Pa cyst and therefore root balls devoid of cysts indicated that the initial single cyst inoculum was Ro.

6.3.4 Experimental Assumptions

A number of assumptions were made during the design of these experiments and attempts were made to test and minimise their influence.

Assumption 1

It was assumed that although the two species were morphologically similar and closely related Ro and Pa were non interbreeding entities and therefore satisfied the species definition of Mayr (1963). This assumption is based on the work of Parrott (1972), Kort and Jaspers (1973), Parrott *et al.* (1975), Franco and Evans (1978), and Mugniery (1979) who all showed with varying degrees of certainty that *G. pallida* was a valid species.

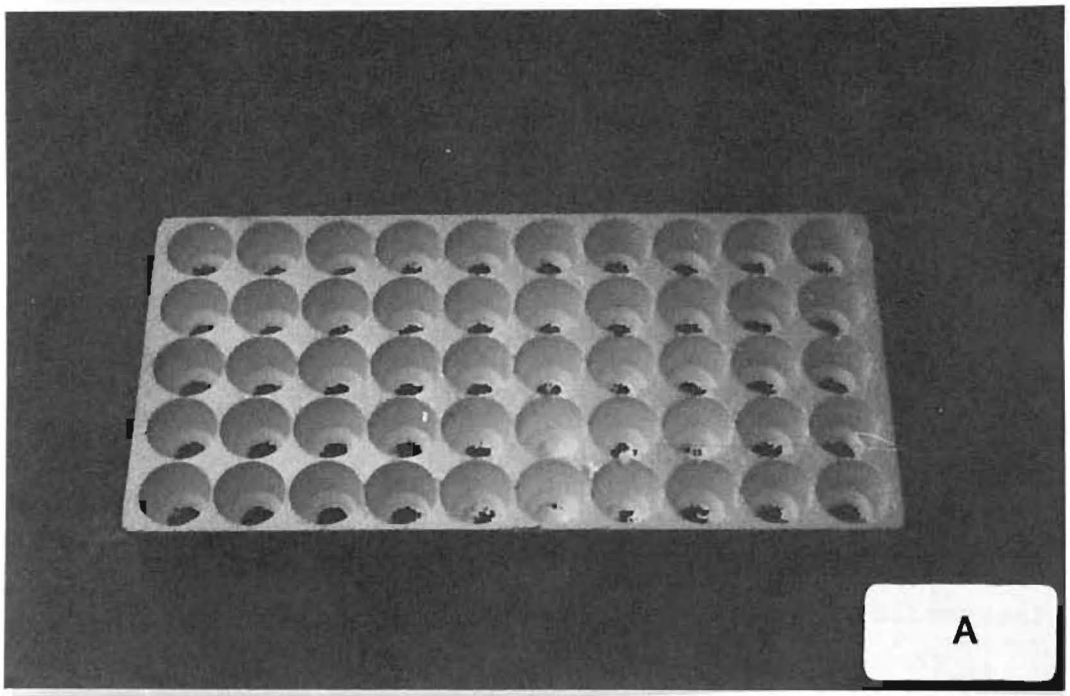
The capacity of the two species to hybridise has been demonstrated in the laboratory but never in the field. Under the environmental conditions prevailing in the South Island of New Zealand it is unlikely that hybridisation will occur to any great extent as results from

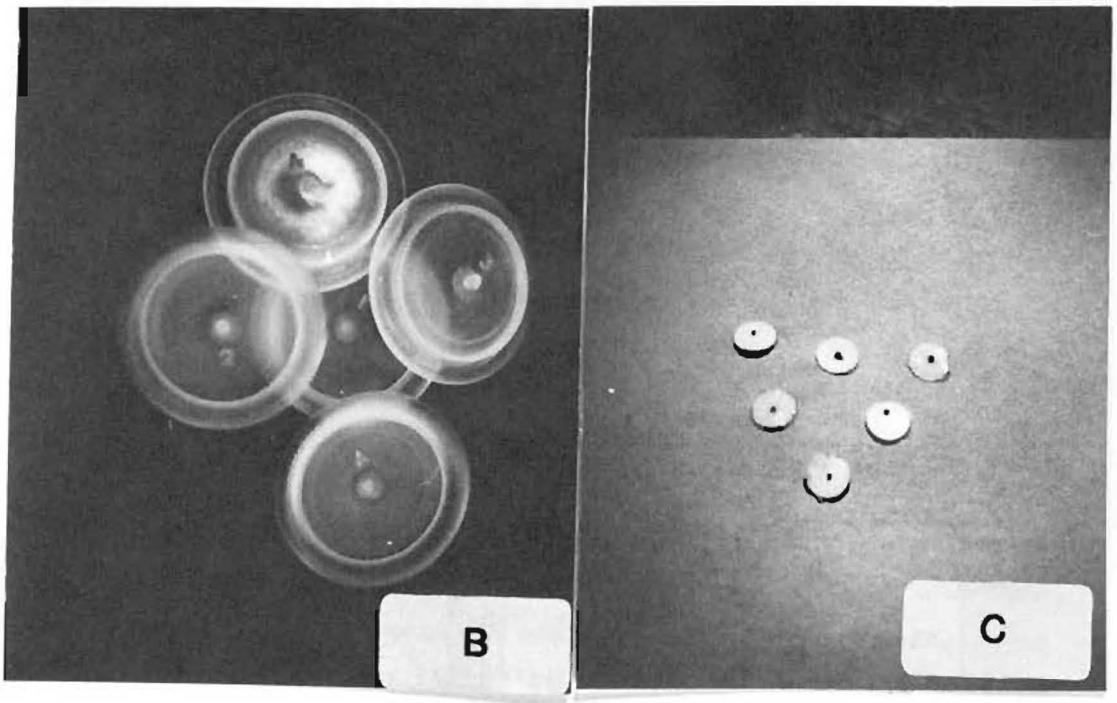
FIGURE 6.1

A. Polystyrene propagating tray used to grow Ro resistant potatoes to distinguish between Ro and Pa progeny in experiments 1 and 2.

B. Plastic wads placed in bottom of polystyrene trays to retain roots and moisture.

C. Single cyst on 4 mm circles of filter paper which were placed on the side of each hole in the propagating tray at tuber planting.


A


B
C

experiments show that L_2 larvae of Pa are slower to hatch than those of Ro (Chapter 5.3.1). This characteristic would isolate the species in the root spatially as well as temporally. Further, Parrott *et al.* (1975) showed that females of one species tend to attract males of the same species and this would reduce the probability of hybridization. Consequently, if hybridization occurred in my experiments it is likely to have been of little consequence to the outcome.

Assumption 2

It was assumed that when produced under identical conditions cysts of both species would hatch with equal efficiency. All inocula were retained in sachets and at harvesting time the sachets from each treatment were recovered. The proportion of unhatched eggs was determined for each ratio set. The proportion of unhatched eggs from ratio set Ro_{100} and Pa_{100} was determined. The mean percent hatch was 63.0 $\pm$SE13.9 and 85.2 $\pm$SE6.4 for Pa and Ro respectively. These values were not significantly different ($P>0.05$). The mean effective inoculum was calculated as 7.4 eggs/ml. This value was used in all subsequent calculations.

Assumption 3

It was assumed that both species were able to multiply on the same host cultivar. To test multiplication efficiency on different hosts, three susceptible cultivars were infested separately with egg suspensions of Pa and Ro. Inoculum density was 10.0 eggs/ml soil and infested plants were grown in a glasshouse at 17.5° $\pm$ 1°C. The cysts produced were recovered at plant senescence.

Fecundity and multiplication factors were calculated from the cysts produced and are shown in Table 6.3. Significant differences ($P<0.05$) in multiplication factors were found between Pa and Ro on each host plant. Multiplication of Pa was always lower than Ro for all cultivars tested. Similarly, Ro had a higher fecundity (eggs/cyst) than Pa.

It is concluded that although multiplication rates between species differed, both species had an equal opportunity to establish on the same cultivar. Therefore differences in multiplication were primarily the result of variations in species fecundity. Although nematodes on Ilam Hardy had the lowest multiplication rate it was used in my work as it is the main commercial cultivar grown in New Zealand.

TABLE 6.3

Mean number of cysts/100 ml of soil, fecundity and multiplication factors for two species produced on three susceptible cultivars. KAT = Katahdin, AB = Arran Banner, IH = Ilam Hardy (n=5).

Cultivar	Cysts produced (per 100ml)		Fecundity (eggs/cyst)		Multiplication factor	
	Pa	Ro	Pa	Ro	Pa	Ro
	mean (± SE)	mean (± SE)	mean (± SE)	mean (± SE)	mean	mean
KAT	124(±10.6)	148(±12.3)	243(± 2.4)	275(±28.2)	30.1	40.7
AB	96(±11.2)	136(±21.7)	246(±17.3)	323(±14.8)	23.6	43.9
IH	103(± 9.0)	122(± 8.3)	151(± 7.6)	194(± 2.9)	18.4	24.0

Assumption 4

It was assumed that after 12 months storage all cysts would hatch when stimulated by a host plant root exudate.

Dunn (1954, 1962) demonstrated that extended dry storage of cysts reduced the level of egg hatch. He also showed that this effect could be minimised if the cysts were preconditioned prior to use in a warm (35°C) moist environment for 21 days. Because cysts produced in my experiments were dry stored for 12 months, they were preconditioned in this way before use.

The efficiency of the treatment was tested on the progeny of experiments 1 and 2. A total of 200 cysts of Ro and Pa from the Ro_{100} and Pa_{100} ratio sets were inoculated individually on to 100 Ilam Hardy and 100 Maris Anchor plants. Complete hatching did not occur in spite of preconditioning (Table 6.4). Although percentage hatch was reduced in the progeny of both experiments there was no significant difference within each experiment between percent hatch of Ro and Pa or between the host cultivars. The negative response of Ro on Maris Anchor was expected. However, the significant difference ($P<0.05$) between the percentage hatch in experiments 1 and 2 was not expected. A possible explanation for this result is that the soil used in the glasshouse experiment became drier towards the end of the experiment than the soil in the field experiment. If so, this influence on the cyst seems to have persisted in spite of their being stored under the same conditions for 12 months after harvest. Correction factors were calculated (Table 6.4) to remove the bias produced by incomplete cyst hatching. This was particularly important as otherwise a non hatching Pa cyst could be interpreted as an Ro cyst if it was planted with a Ro resistant potato.

TABLE 6.4

Mean percentage of plants producing white cysts of Pa and Ro on resistant and susceptible potato plants and the factors calculated to correct for partial cyst hatching. (IH = Ilam Hardy, MA = Maris Anchor.)

Species and cultivar	Percent positive	Calculated correction factor
Experiment 1		
Pa IH	51.2 a	
Ro IH	61.6 a	x 1.91
Pa MA	53.4 a	
Ro MA	0.00	
Experiment 2		
Pa IH	26.6 a	
Ro IH	32.9 a	x 3.81
Pa MA	25.8 a	
Ro MA	0.00	

Within each experiment, values followed by the same letter were not significantly different at the 5% level.

6.3.5 Analysis of results

To study interactions between populations, known numbers of animals of two species may be released into a resource limited environment and subsequent changes in composition, death rate, and or birth rate can be recorded over a number of generations.

Such an approach is not possible with potato cyst nematodes because of the difficulty in discriminating between generations. Single generation experiments repeated at a range of proportions avoided this problem. De Wit's (1960) ratio diagram method (in Harper, 1977), which involves comparisons of species ratios at the beginning and end of an experiment was used to analyse the results of both experiments. It is sensitive to changes in proportions, and detects frequency dependent interactions (Harper, 1977). The slope and position of the lines produced by ratio diagram analysis fit one of four types of response, and show the status of the interacting populations.

In a Type I response, the ratio of both species remains unaltered after a period of growth together.

In a Type II response, one or other species is disadvantaged regardless of the species ratio and ultimately will go to extinction.

In a Type III response, the initially less abundant species is at an advantage and increases but it is not possible to specify which species will have the advantage without specifying the frequency. This is known as a frequency-dependent situation and mixtures will tend to establish an equilibrium between the lower and upper frequencies.

In a Type IV response, the major component has the advantage and no equilibrium between frequencies will be maintained even though the outcome is frequency-dependent.

6.4 RESULTS

6.4.1 Experiment 1

Mean cyst numbers (per 100 ml of soil) were obtained for each ratio class and overall multiplication factors for each class were calculated. Results are presented in Table 6.5. The effective inoculum for this experiment was 7.4 eggs/ml of soil.

TABLE 6.5

Mean number of cysts/100 ml of soil, mean fecundity and multiplication factors for all ratio classes based on an effective inoculum of 7.4 eggs/ml soil (n=4).

Ratio class Pa Ro	cysts/100ml	Fecundity (eggs/cyst)	Multiplication factor
Pa : Ro	mean (± SE)	mean (±SE)	
100: 0	72.0(± 6.5)	295.5(± 7.2)	28.7
99: 1	52.3(± 3.9)	314.8(±12.7)	22.0
90: 10	57.7(± 8.5)	299.1(± 8.0)	23.9
50: 50	95.3(±16.3)	285.7(±11.8)	37.1
10: 90	174.2(±52.0)	302.1(± 9.2)	72.5
1: 99	134.0(±15.6)	308.8(± 8.7)	55.6
0:100	120.0(± 9.7)	309.3(±16.3)	49.5

Total cyst numbers increased as the proportion of Ro in the original mixture increased. Significant differences ($P<0.05$) were found

between Pa_{100} and Ro_{100} populations but there was no difference when the ratio classes contained a high proportion of the same species (i.e. Ro_{90}, Ro_{99}; and Pa_{90}, Pa_{99}). No significant differences were found between fecundity (eggs/cyst) levels of all ratio classes, although there was a tendency for higher fecundity to occur in mixtures with Ro dominant.

The percentage of Pa cysts and cyst percentages corrected for incomplete hatch (Table 6.4) are shown in Table 6.6.

TABLE 6.6

Mean observed percentage of plants with Pa cysts in each ratio class. Percentage corrected to account for incomplete hatch.

Ratio class Pa : Ro	Percentage of plants with Pa cysts. mean (±SE)	Corrected percentages (observed % x1.91)
100: 0	52.3(±6.1)	99.9
99: 1	47.0(±5.9)	89.9
90: 10	25.5(±7.2)	48.7
50: 50	5.8(±1.2)	11.2
10: 90	2.4(±0.4)	4.4
1: 99	0.0	0.0
0:100	0.0	0.0

Corrected values for the percentage of Pa in the final ratio set were generally lower than in the original ratio class figures and indicated that the two species were interacting so that the proportion of Pa in the progeny was reduced.

The number of cysts/100 ml for both species in each ratio class are shown in Table 6.7

TABLE 6.7

Numbers of cysts produced by each species during interaction experiments with different ratio classes.

Ratio class Pa : Ro	Progeny (cysts/100 ml)	Percentage of Pa	Cysts/100 ml according to species	
			Pa	Ro
100: 0	72.0	99.9	72	0
99: 1	52.3	89.9	47.1	5.3
90: 10	57.7	48.7	28.1	29.6
50: 50	95.3	11.2	10.6	84.8
10: 90	174.2	4.4	7.6	166.7
1: 99	134.0	0	0	134.3
0:100	120.0	0	0	120.0

Calculated multiplication factors, and fecundity values for each ratio class are shown in Table 6.8. Initial effective density of the inoculum for each ratio class is also presented.

TABLE 6.8

Initial effective egg density, progeny fecundity and segregated species multiplication factors in experiment 1.

Ratio class	Effective egg density (eggs/ml)		Fecundity (eggs/cyst)	Multiplication factor	
Pa : Ro	Pa	Ro		Pa	Ro
100: 0	7.4	0.0	295.5	28.6	0.0
99: 1	7.3	0.1	314.8	20.1	225.3
90: 10	6.7	0.7	299.1	12.5	119.6
50: 50	3.7	3.7	285.7	8.2	65.4
10: 90	0.7	6.7	302.1	31.1	75.5
1: 99	0.1	7.3	308.8	0.0	56.5
0:100	0.0	7.4	309.3	0.0	50.1

Multiplication factors for Pa ranged from 8.2 - 31.1 and were greatest at Pa:Ro ratios of 100:0 and 10:90. Multiplication factors were up to seven times higher in Ro and were greatest at Pa:Ro ratios of 99:1 and 90:10.

Ratios of the species based on eggs/ml of soil, for initial and final egg densities in all ratio classes are shown in Table 6.9. Arithmetic values were logarithmically transformed (Harper 1977), and a linear regression was performed on the data. A significant fit ($P<0.05$) was obtained for all data points in the regression model (Figure 6.2).

FIGURE 6.2

Input-output ratio diagram showing effect of competition between Ro and Pa in a field situation. (Initial total egg density, 7.4 eggs/ml)

Straight line fitted by least squares line of best fit.

diamonds	=	observed data
solid line	=	fitted regression line
long dashed line	=	line of non interaction (a=1)

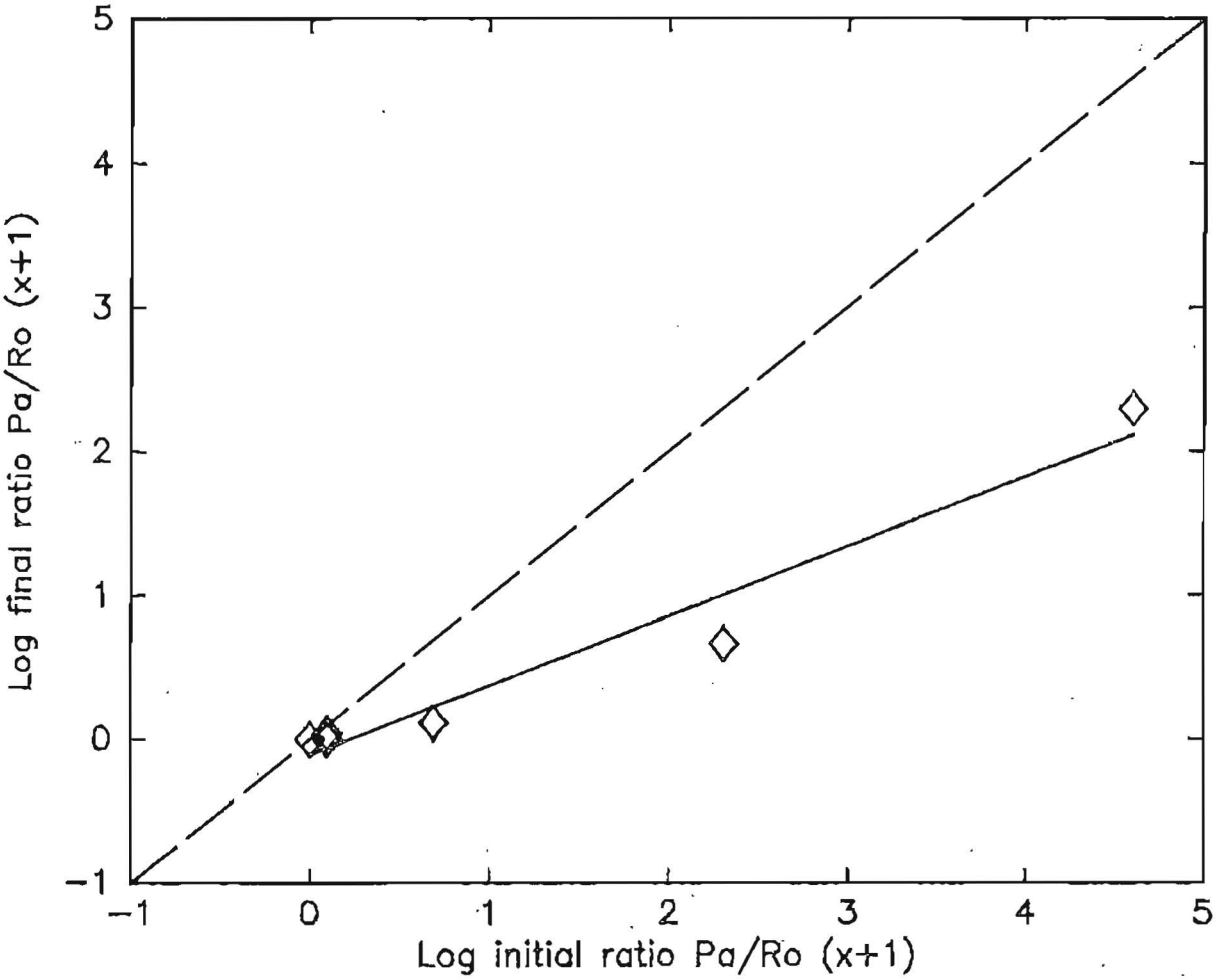

5
4
3
2
1
0
−1
−1
0
1
2
3
4
5
Log final ratio Pa/Ro (x+1)
Log initial ratio Pa/Ro (x+1)

TABLE 6.9

Egg numbers and interspecific egg ratios for all ratio classes at the start and end of experiment 1.

Ratio class Pa : Ro	Initial density (eggs/ml)		Final density (eggs/ml)		Ratio of species (initial density)	Ratio of species (final density)
Pa : Ro	Pa	Ro	Pa	Ro	Pa/Ro	Pa/Ro
100: 0	7.4	0.0	212.7	0.0	-	-
99: 1	7.3	0.1	148.2	16.6	98.9	8.9
90: 10	6.7	0.7	84.0	88.5	9.0	0.94
50: 50	3.7	3.7	30.2	242.2	1.0	0.12
10: 90	0.7	6.7	22.9	503.6	0.11	0.04
1: 99	0.1	7.3	0.0	414.7	0.01	0.0
0:100	0.0	7.4	0.0	371.1	-	-

A change in proportions of the two species was found in a single generation. The interaction was partially described by a type III model. Ro, the initially less abundant species in Pa:Ro 99:1 90:10 ratio classes increased in the final species ratio. On the other hand, Pa in a similar initial minority (10:90 1:90) did not increase their representation in the final ratio. Although Pa did not increase in the final population of any ratio sets there was a tendency for Pa in low proportions e.g. at 10:90 to perform better than when present as a high proportion of the ratio set e.g. at 99:1 90:10. This suggests that a response similar to a type III model may have occurred with Pa but at a lower non-detectable level.

6.4.2 Experiment 2

Mean numbers of cysts of both species produced per 100 ml of soil for all ratio classes at four egg densities are presented in Table 6.10.

TABLE 6.10

Mean number of cysts produced/100 ml of soil for four inoculum densities and seven ratio classes.

Ratio classes Pa : Ro	Initial density			
	0.3 eggs/ml	2.4 eggs/ml	19.2 eggs/ml	153 eggs/ml
	mean (±SE)	mean (±SE)	mean (±SE)	mean (±SE)
100 : 0	0.17(±0.10)	0.96(±0.14)	17.1(± 1.55)a	56.2(± 8.62)a
99 : 1	0.12(±0.08)	1.08(±0.98)	11.1(± 1.40)b	55.3(± 3.98)a
90 : 10	0.33(±0.24)	1.50(±0.40)	20.1(± 3.18)ac	77.4(± 7.18)b
50 : 50	0.42(±0.03)	1.42(±0.29)	31.6(± 1.31)cd	131.2(±15.90)c
10 : 90	0.62(±0.08)	6.95(±1.32)	66.0(±14.81)d	234.8(±26.38)d
1 : 99	0.45(±0.46)	11.95(±0.81)	97.2(±19.90)d	234.6(±43.70)d
0 : 100	0.83(±0.14)	21.75(±1.44)	95.8(±17.41)d	303.2(±28.20)d

In each column, data followed by the same letter are not significantly different at the 5% level.

Insufficient cysts were produced from the 0.3 and 2.4 eggs/ml inoculations to allow useful analysis, and as a result, analysis was restricted to the progeny of 19.2 and 153 eggs/ml density classes. Numbers of cysts produced per 100 ml of soil (Table 6.10) were not significantly different ($P>0.05$) between ratio classes with a high proportion of Ro. However, when the proportion of Ro dropped to 0.5 and below, a significant decrease in the total number of cysts produced was found.

Fecundity and multiplication factors calculated for the two density groups are shown in Table 6.11.

TABLE 6.11

Fecundity and multiplication factors for the progeny of all ratio classes at two densities (n=4).

Ratio class Pa : Ro	Fecundity Initial density		Multiplication factor Initial density	
	19.2 mean (±SE)	153.0 mean (±SE)	19.2	153.0
100:0	193.5(±31.0)	178.0(±24.9)	1.7	0.7
99:1	160.2(±29.7)	177.0(±44.9)	0.8	0.5
90:10	145.7(±30.8)	128.0(±14.7)	1.5	0.6
50:50	124.5(±32.0)	161.5(±34.9)	1.9	1.3
10:90	146.2(±42.7)	187.0(±34.8)	5.0	2.8
1:99	261.0(±61.0)	208.0(±40.4)	13.0	3.1
0:100	112.7(±42.0)	181.0(±27.7)	8.6	3.4

No significant differences ($P>0.05$) in cyst fecundity were found between different ratio classes within the density groups or between the two density groups for the same ratio class.

Multiplication factors increased with an increase in the proportion of Ro in the mixture and were higher in the 19.2 than the 153.0 eggs/ml density group.

The percentage of Pa cysts in each situation and the percentages after correction for cyst dormancy are shown in Table 6.12.

TABLE 6.12

The mean percentage of plants with Pa cysts at each density and in each ratio class. Percentages corrected to account for incomplete hatch.

Ratio class Pa:Ro	Percentage with cysts initial density		Corrected percentage (observed % x 3.8)	
	19.2 (mean ±SE)	153.0 (Mean ±SE)	19.2	153.0
100 : 0	26.9(±4.1)	28.5(±3.8)	102.4	98.4
99 : 1	24.1(±4.1)	22.7(±3.5)	91.8	86.8
90 : 10	19.5(±1.0)	17.5(±1.4)	74.2	67.0
50 : 50	10.1(±0.68)	6.22(±0.75)	38.5	23.7
10 : 90	2.9(±0.51)	2.54(±0.40)	11.0	9.7
1 : 99	0.44(±0.17)	0.27(±0.27)	1.6	1.0
0 : 100	0.0	0.0	0.0	0.0

The corrected values for Pa in each ratio class at each density were compared with the original ratio class values. A large difference was found with respect to the ratio classes between Pa:Ro 99:1 and 50:50, but a lesser difference was found for Pa:Ro 10:90 and 1:99.

The numbers of Ro present in the progeny were calculated from total numbers of cysts produced and the proportion of Pa in the samples. Numbers of Pa and Ro in each ratio class are presented in Table 6.13.

TABLE 6.13

Numbers of cysts produced by each species in different ratio classes at two initial densities.

Ratio class Pa : Ro	Mean numbers of cysts/100 ml (mean ±SE) (both species combined)		Number of cysts Pa and Ro per 100 ml (mean)			
Initial density	19.2	153	19.2		153	
			Pa	Ro	Pa	Ro
100 : 0	17.1(±1.55)	56.2(±8.62)	17.1	0	56.2	0
99 : 1	11.1(±1.40)	55.3(±3.98)	10.1	1.0	48.0	7.3
90 : 10	20.08(±3.18)	77.4(±7.18)	14.9	5.1	51.8	22.5
50 : 50	31.6(±1.31)	131.2(±15.90)	12.1	19.4	31.1	100.1
10 : 90	66.0(±14.81)	234.8(±26.38)	7.3	58.7	22.8	212.0
1 : 00	97.2(±19.9)	234.6(±43.70)	1.5	95.7	2.3	232.2
0 :100	95.8(±17.41)	303.2(±28.20)	0.0	95.8	0.0	303.2

TABLE 6.14

Initial effective egg densities for both species, fecundity of progeny (from Table 6.11) and multiplication factors for both Pa and Ro at two initial densities; 19.2 and 153 eggs/ml.

19.2 eggs/ml

Ratio class Pa : Ro	Initial effective density (eggs/ml) Pa : Ro		Fecundity (eggs/cyst)	Multiplication factor Pa : Ro	
100 : 0	19.2	0	193.5	1.7	0
99 : 1	19.0	0.2	160.2	0.8	8.0
90 : 10	17.2	2.0	145.7	1.3	3.7
50 : 50	9.6	9.6	124.5	1.6	2.5
10 : 90	2.0	17.2	146.2	5.2	5.0
1 : 99	0.2	19.0	261.0	19.6	13.1
0 : 100	0.0	19.2	182.7	0.0	9.1
153.0 eggs/ml					
100 : 0	153.0	0.0	178.0	0.65	0.0
99 : 1	151.5	1.5	177.0	0.56	8.6
90 : 10	137.7	15.3	128.0	0.48	1.9
50 : 50	76.5	76.5	161.5	0.65	2.1
10 : 90	15.3	137.7	187.0	2.8	2.9
1 : 99	1.5	151.5	208.0	3.2	3.2
0 : 100	0.0	153.0	181.0	0.0	3.6

TABLE 6.15

Initial, and final densities (eggs/ml), and ratio sets for both Pa and Ro at initial densities of 19.2 and 153.0 eggs/ml.

Ratio class	Initial density (eggs/ml)		Final density (eggs/ml)		Ratio of species (initial density)	Ratio of species (final density)
19.2 eggs/ml						
Pa : Ro	Pa	Ro	Pa	Ro	Pa/Ro	Pa/Ro
100: 0	19.2	0.0	33.0	0.0	0.0	0.0
99: 1	19.0	0.2	16.1	1.6	95.0	10.0
90: 10	17.2	2.0	23.0	7.4	8.6	3.11
50: 50	9.6	9.6	15.0	24.1	1.0	0.62
10: 90	2.0	17.2	10.7	85.8	0.11	0.12
1: 99	0.2	19.0	3.9	249.7	0.01	0.02
0:100	0.0	19.2	0.0	175.0	0.0	0.0
153.0 eggs/ml						
100: 0	153.0	0.0	100.0	0.0	0.0	0.0
99: 1	151.5	1.5	84.9	12.9	101.0	6.5
90: 10	137.7	15.3	66.3	28.8	9.0	2.3
50: 50	76.5	76.5	50.2	161.6	1.0	0.31
10: 90	15.3	137.7	42.6	396.4	0.11	0.10
1: 99	1.5	151.5	4.8	482.9	0.01	0.01
0:100	0.0	153.0	0.0	548.7	0.0	0.0

Multiplication factors for both species in each ratio class were calculated from the values presented in Table 6.13 and are presented in Table 6.14. In all ratio classes and at both initial densities, multiplication factors were low and never exceeded x 20. In each ratio class multiplication generally was higher at the lower (19.2 eggs/ml) density.

Initial and final egg densities for both species were calculated as in experiment 1 and are shown in Table 6.15. As in experiment 1 the ratio of the species in the initial and final densities for both overall density groups were log-transformed prior to a linear regression analysis. A significant fit ($P<0.05$) was obtained for all data points at each overall density (Figure 6.3).

The regression lines for both density groups had similar slopes and as in experiment 1 were below the line of non-interaction ($a=1$). However, when in a more favourable environment Pa as the less abundant species (10:90 1:99) was able to maintain or increase its representation in the final species ratio. In the same environment Ro, as the less abundant species was only able compete in the 99:1 ratio class when at the lower (19.2) eggs/ml overall density. From the regression lines it is apparent that the slopes obtained for the two density groups are the same.

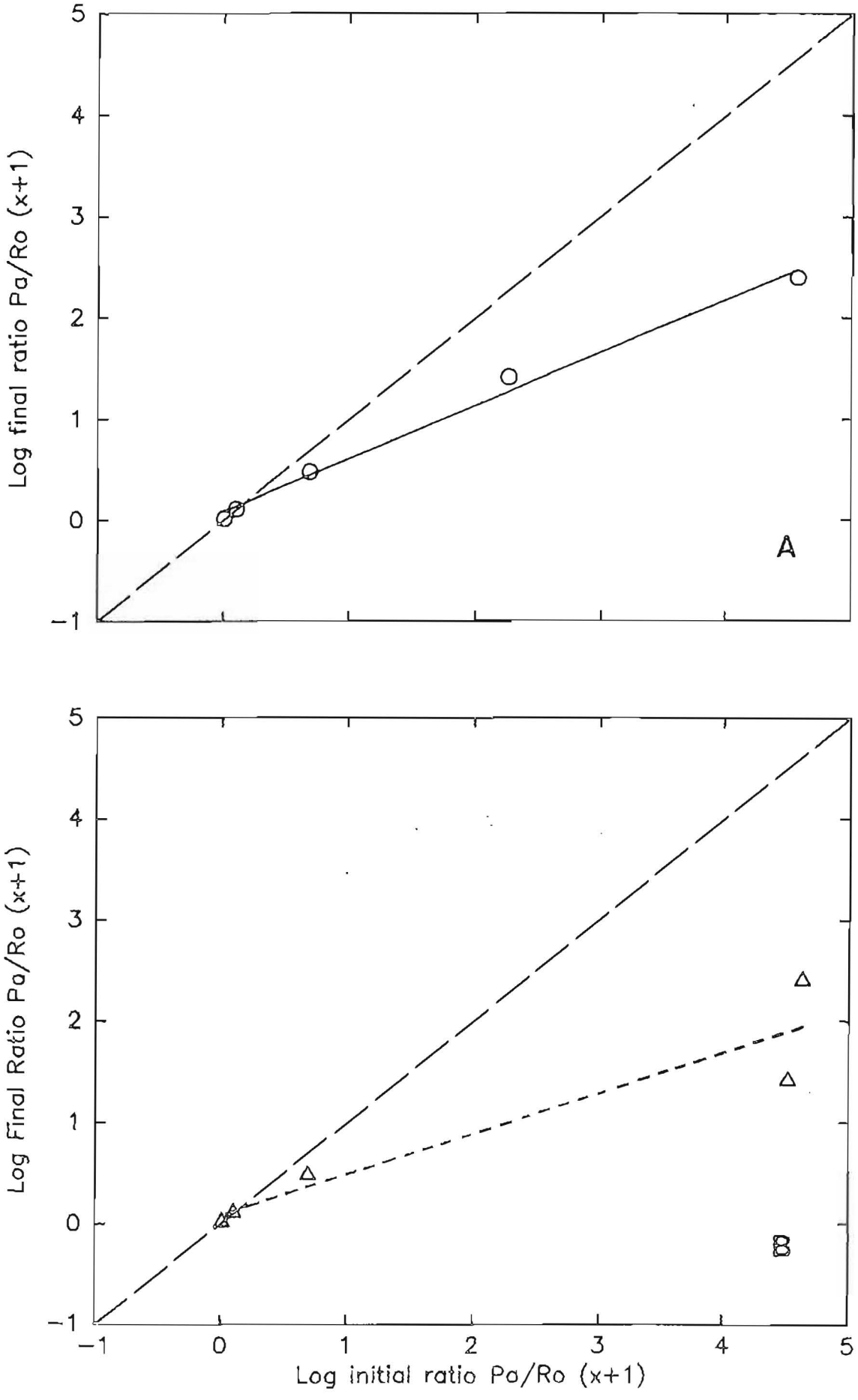
FIGURE 6.3

Input-output ratio diagram showing the effect of competition between Ro and Pa at two densities in a controlled environment.

A	=	Initial overall density 19.2 eggs/ml
B	=	Initial overall density 153.0 eggs/ml
long dashed line	=	line of non-interaction (a=1)

Straight lines fitted by least squares line of best fit.

circles	=	observed data at 19.2 eggs/ml
solid line	=	fitted regression line at 19.2 eggs/ml
triangles	=	observed data at 153 eggs/ml
short dashed line	=	fitted regression line at 153 eggs/ml


Log final ratio Pa/Ro (x+1)
5
4
3
2
1
0
−1
A
Log Final Ratio Pa/Ro (x+1)
5
4
3
2
1
0
−1
B
−1
0
1
2
3
4
5
Log initial ratio Pa/Ro (x+1)

6.5 DISCUSSION

Multiplication factors calculated for experiments 1 and 2 differed markedly. Those for the Pa_{100} and Ro_{100} ratio classes in experiment 1 were similar to those of other populations maintained under similar field conditions (Table 5:16), but nematode multiplication in experiment 2 was much lower than expected. This difference was largely the result of delayed inoculation into the host root system (Appendix XVIII). Significant reductions in the Ro multiplication factor occurred after 30 days but a significant decrease in Pa multiplication was observed after only eight days. There was no significant difference in the multiplication of both Pa and Ro at any one time.

In experiment 2, overall multiplication was influenced by inoculum density and multiplication was lower at higher densities. Differences in the proportion of Pa in initial and final Pa:Ro mixtures showed that interactions between the two species occurred and overall multiplication was strongly influenced by the proportions in the initial mixture. Analysis of the initial and final ratio sets for both experiments showed that Ro was more successful as the final number of Ro eggs in the soil was higher than in the initial level. This increase was at the expense of Pa in the mixture.

The slopes of the ratio set lines in the two experiments were similar and a consistent frequency dependent response was observed. All slopes tended to converge at zero and the y intercepts for all experiments were not significantly different from zero. In the field based experiment (experiment 1) the ratio line was well below the line of no advantage (a=1) for all ratio classes. Extrapolation of the line showed that there was a point at which the two lines converged and where the Pa and Ro populations would be in equilibrium. This point was reached when Pa was at a very low frequency.

In Section 5.3.8, I showed that Ro hatched earlier from the cyst and spent less time in the soil than Pa before establishing in host roots. Both these characteristics make Ro a more effective parasite in many South Island field situations. These hatching and establishing characteristics can also account for some of the observed frequency dependent responses which show that regardless of the species, the minority species in the mixture always maintained or improved its representation in the mixture.

Let us consider the situation where Ro is the more abundant species. When stimulated it will hatch before Pa and become established more quickly in the roots. Because of its lower mortality in the soil a greater number of larvae will establish in the roots and occupy most

of the available sites. There will be some intraspecific competition and this may result in reduced multiplication. Pa as the less abundant species will hatch at a later date and colonise a different set of roots (most likely different in time and space). For these reasons, Pa is unlikely to compete directly with Ro for sites and because of relatively low numbers will exhibit limited intraspecific interactions. The effect of there being fewer suitable sites in the remaining root system will most likely be minimised by the low larval numbers. Consequently, Pa multiplication will be higher.

In the converse situation, the more abundant Pa will be slower to colonise and as usual Ro will establish earlier. However, because initial density of Ro is low there should be little intraspecific competition and hence a higher rate of Ro multiplication can be achieved. Pa will establish after Ro and take up a range of root sites not occupied by Ro. Some of these sites will be less desirable and this combined with some degree of intraspecific competition will depress the multiplication of Pa.

Experiment 2 demonstrated the same frequency dependent responses as experiment 1 but showed that overall density could modify the frequency dependent effect. At low densities there was an improvement in the multiplication of Pa over a wide range of Pa:Ro ratios. This was probably the result of reduced intraspecific competition (by Pa) since there would be more root sites available for colonisation by Pa even after Ro had established.

In both experiments 1 and 2, the equilibrium point was not determined but Cole and Howard (1962) indicated that two species can be present in a field situation, one at a very low and often nondetectable level. Thus, after a number of years Cole and Howard found Pa when Ro resistant potatoes were planted, yet it had not been observed before. As in their study, I found that the numbers of the normally dominant Ro had to be reduced in absolute terms before Pa could compete.

6.6 SUMMARY

The experimental results obtained allow a number of tentative generalisations to be made as follow:-

1. In the silt soils of Canterbury Ro is more successful than Pa.

2. Frequency dependent responses between the two species were detected in both field and glasshouse trials. The minority species was able to maintain itself in the mixture.

3. In a mixture of two species the proportions of the two species will change until an equilibrium is achieved and in the Canterbury situation this will occur at a point where the proportion of Pa present is very low.

4. The competitiveness of Pa is improved when the total density of the mixture is reduced. There is a suggestion that the equilibrium point between the two species is higher at lower overall densities.

CHAPTER 7

POPULATION CHANGES IN THE ABSENCE OF A HOST

7.1 INTRODUCTION

Attrition in viable egg numbers occurs within all cysts in the absence of host stimulation. Attrition has been described also as reduction (Shepherd, 1962b), decrement (Grainger, 1959) and population decrease (Jones and Kempton, 1978).

The measurement of attrition rate is an integral part of a nematode management program as the rate of attrition influences the required duration of a rotational cropping pattern (Nusbaum and Ferris, 1973). Most countries practice rotation in some form, (Southey, 1978) so that the number of live nematodes can be reduced to a level sufficiently low that a subsequent host crop will not suffer serious damage (Brown, 1978).

Rates of natural attrition vary in different countries (Fenwick, 1955, 1956; Grainger, 1959; Oostenbrink, 1952; Cooper, 1954; Cole and Howard, 1959; Reinmuth and Schmidt, 1959; Toxopeus, 1959; Schlüter, 1976; Oydvin, 1978) and annual percentage losses reported under fallow or non host crops range from 4% to 95%.

Geographical differences have been noted. In hot countries such as Israel, attrition rate is very high (Cohn et al., 1970), whereas in cooler countries such as Norway (Oydin, 1978) much lower rates have been reported.

Attrition rates for the Pa_2 population at Pukekohe as determined by Foot et al. (1980) were higher (70% per annum) than in most temperate countries. Both the climate and cropping patterns used in the South Island are markedly different from those at Pukekohe. Pukekohe has a virtually frost free, maritime, subtropical climate and the traditional potato crop is very early, being planted in April-May and harvested in August-September.

It is unlikely therefore that attrition rates determined from the Pukekohe population could be appropriately used as a guideline for a South Island management program. The presence of two species further complicates the South Island situation as there is no information regarding possible differences in attrition rates between the two species.

In the present study, attrition rates of both species were examined and compared in silt and peat soils in Canterbury. At Outram the attrition rate of Ro (the only species detected) was also determined because the soil type is different from that in Canterbury (see Appendices I, II and III).

There is no information on whether different sized cysts have different attrition rates. Therefore, to determine whether cyst size influences attrition rate, all populations were subdivided according to cyst size and the size classes were examined separately.

7.2 METHODS

7.2.1 Preparation of populations

Pure populations of Ro_4 and Pa_3 were established at Lincoln during the 1978-79 growing season. Both species were grown under identical conditions as outlined in Chapter 2, so that large numbers of new cysts were available.

Attrition rates were determined on three arbitrarily chosen cyst size classes which spanned the entire size range; 250-350 micrometres diameter (small), 350-500 micrometres (medium), 500-850 micrometres (large). Populations were divided into the three sizes, then reconstituted, so that equal numbers of cysts of each size were present for future sampling. Egg status (numbers live, dead and hatched) in each size class for each species is shown in Table 7.1.

Uninfested soil from the three research areas, S4, Cranford St. and Outram was collected and cysts were mixed with the soil to give a mean density of 31.5 cysts/100ml soil. One quarter of this infested soil was placed into each of four terylene bags. They were returned to their original site of collection and buried with the tops of the bags open and contents flush with the soil surface (Figure 7.1).

Because of quarantine requirements, Pa_3 was not introduced to Outram. Population codes for both species at each location are listed in Table 7.2.

FIGURE 7.1

Terylene bag in soil with top open and contents flush with the surrounding soil.

TABLE 7.1

Egg status (numbers of eggs/cyst) in three size classes of cysts belonging to the two species used to establish the population attrition study at three locations in the South Island (n=4). [250-350 micrometres = small, 350-500 micrometres = medium, 500-850 micrometres = large].

	Cyst size		
	Small mean (±SE)	Medium mean (±SE)	Large mean (±SE)
	Species Ro		
No. Live	46.0(±6.4)	96.9(±9.2)	385.0(±27.1)
No. Dead	12.0(±1.1)	22.0(±2.2)	9.3(±15.0)
No. Hatched	7.0(±2.1)	7.9(±4.2)	6.9(±8.4)
	Species Pa		
No. Live	38.0(±4.8)	155.0(±6.9)	260.0(± 11.7)
No. Dead	9.0(±1.9)	21.0(±2.5)	57.0(±10.1)
No. Hatched	4.0(±6.2)	11.7(±4.8)	26.9(±13.6)

TABLE 7.2

Population codes for the two nematode species at the three locations.

Population code	Species	Location	Soil type
RoS4	Ro_4	S4 Lincoln	Silt
PaS4	Pa_3	S4 Lincoln	Silt
RoC	Ro_4	Cranford St.	Peat
PaC	Pa_3	Cranford St.	Peat
RoO	Ro_4	Outram	Silt loam

7.2.2 Sampling program

The experiment was set up in July 1979 and terminated in July 1981. Samples were taken if possible in January, April, July and October. On each occasion all four bags were lifted from the ground and the infested soil in each bag was throughly mixed before the 100ml sample was taken. Mixing of the soil also simulated the quarterly cultivation program expected under a normal cropping pattern.

Each sample was air dried in the laboratory and the cysts were extracted, divided into the three size classes and counted. Fifteen cysts of each size class were broken open so that eggs contained could be stained with 'Meldolas' solution, for 48h. Live eggs and free-living larvae, dead eggs, and empty egg shells were counted. Free-living larvae and live egg counts were combined to give total viability.

7.2.3 Soil temperature and moisture

Physical characteristics of the soil environment were recorded for the duration of the sampling program (Chapter 2.10). Continuous soil temperature recordings and weekly soil moisture measurements were taken at all three study sites.

7.3 RESULTS

7.3.1 Whole cyst survival

Mean cyst densities for each location are shown in Figure 7.2. All size classes at each location are combined in the figure because there were no significant ($P>0.05$) differences between sizes. The initial rise in numbers of cysts was a reflection of soil consolidation at the beginning of the experiment but over the remaining months no significant reduction in cyst numbers occurred.

7.3.2 Live eggs

Changes in numbers of live or viable eggs are shown in Figure 7.3, and a more rigorous analysis using log-transformed data is shown in Figure 7.4. The regression coefficients and their standard errors are presented in Table 7.3. Ro_4 had a greater loss of viable eggs than Pa_3 in Canterbury, a pattern which was consistent for all but the small cysts. From the twelfth month on, differences in species egg number were significant ($P<0.05$) for large cysts. Rate of attrition of the Ro_4 population at Outram was significantly different ($P<0.05$) from that of the Ro_4 populations in Canterbury but was similar to that exhibited by all Pa_3 populations. Soil type had no obvious effect on attrition rate (Table 7.4) but the large cysts of Ro_4 and Pa_3 showed significant differences in their rate of attrition in both soil types.

FIGURE 7.2

Total number of cysts recovered from 100 ml of soil at the three locations.

circle with solid line	=	Ro at S4
triangle with solid line	=	Pa at S4
circle with short dashed line	=	Ro at Cranford St.
triangle with short dashed line	=	Pa at Cranford St.
circle with long dashed line	=	Ro at Outram

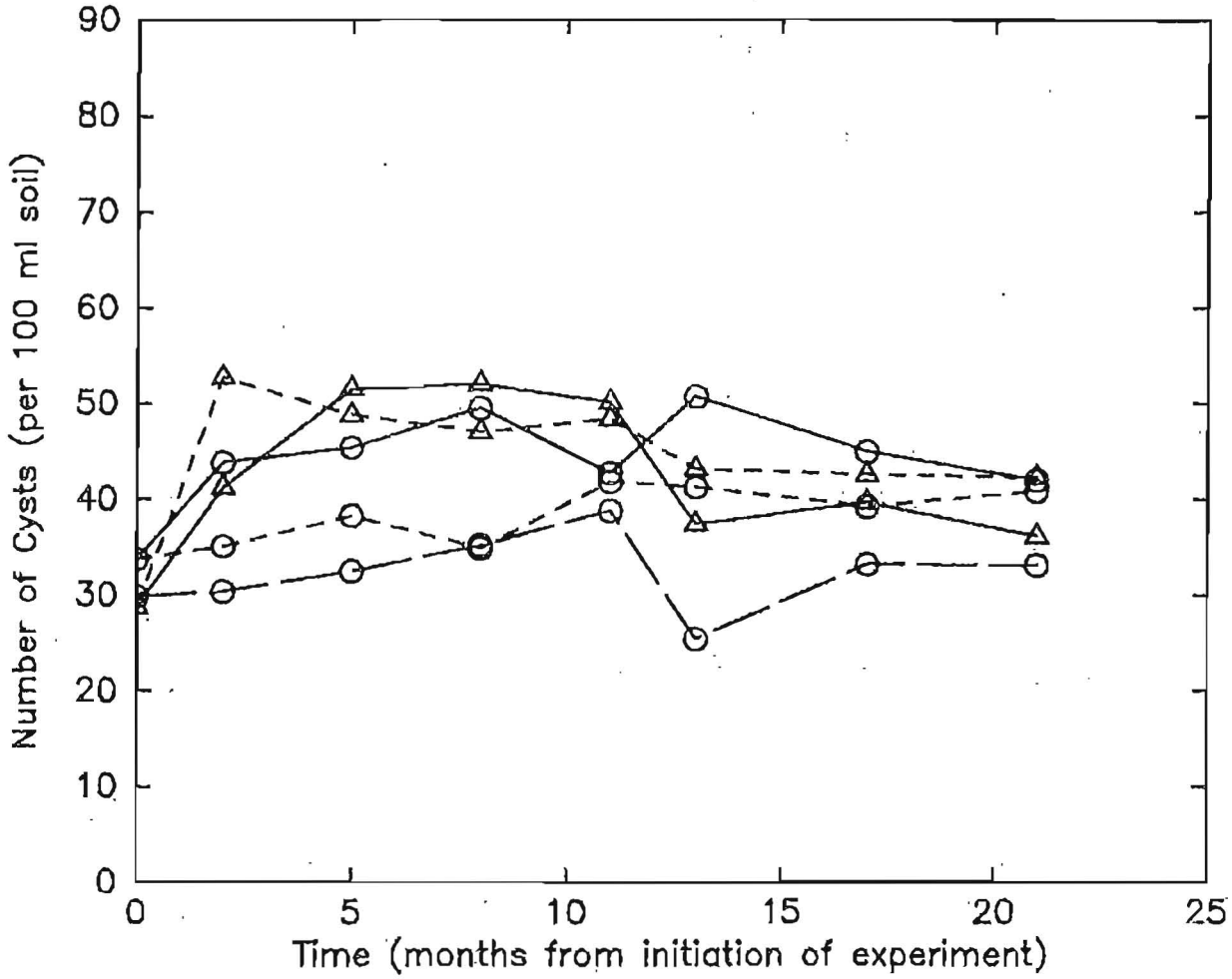

Number of Cysts (per 100 ml soil)
90
80
70
60
50
40
30
20
10
0
0
5
10
15
20
25
Time (months from initiation of experiment)

FIGURE 7.3

Changes in the number of viable eggs per cyst in the two species for three size classes and three locations.

A = large (500-850 micrometres) B = medium (350-500 micrometres)
C = small (250-350 micrometres) D = mean of all sizes

circle with solid line = Ro at S4
triangle with solid line = Pa at S4
circle with short dashed line = Ro at Cranford St.
triangle with short dashed line = Pa at Cranford St.
circle with long dashed line = Ro at Outram

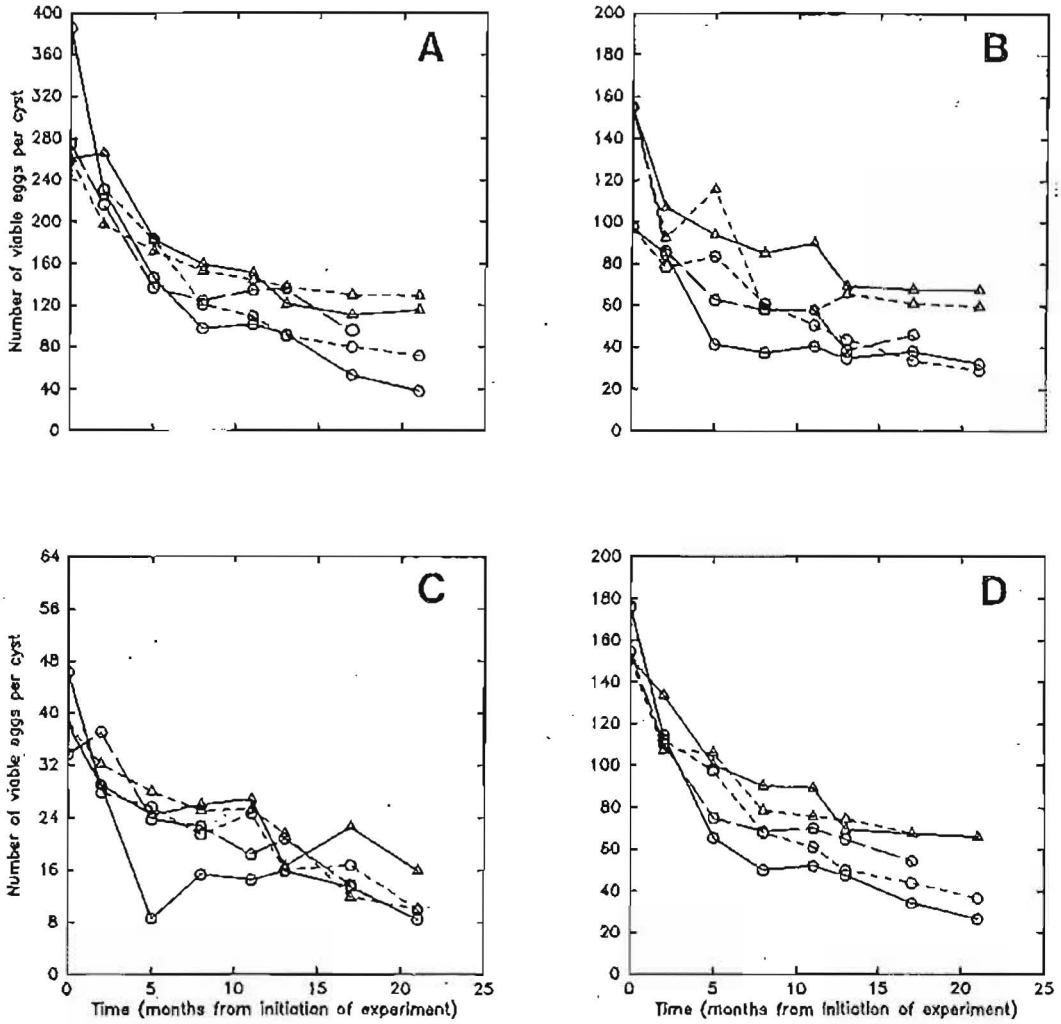

A
B
C
D
Number of viable eggs per cyst
Time (months from initiation of experiment)

FIGURE 7.4

Regression lines fitted to logarithmically transformed data describing the relationship between loss of egg viability and time, for three cyst size classes of two species and three locations.

(For graphical clarity observed data points for all size classes and locations have been deleted).

A = large B = medium C = small D = mean

circle with solid line = Ro at S4
triangle with solid line = Pa at S4
circle with short dashed line = Ro at Cranford St.
triangle with short dashed line = Pa at Cranford St.
circle with long dashed line = Ro at Outram

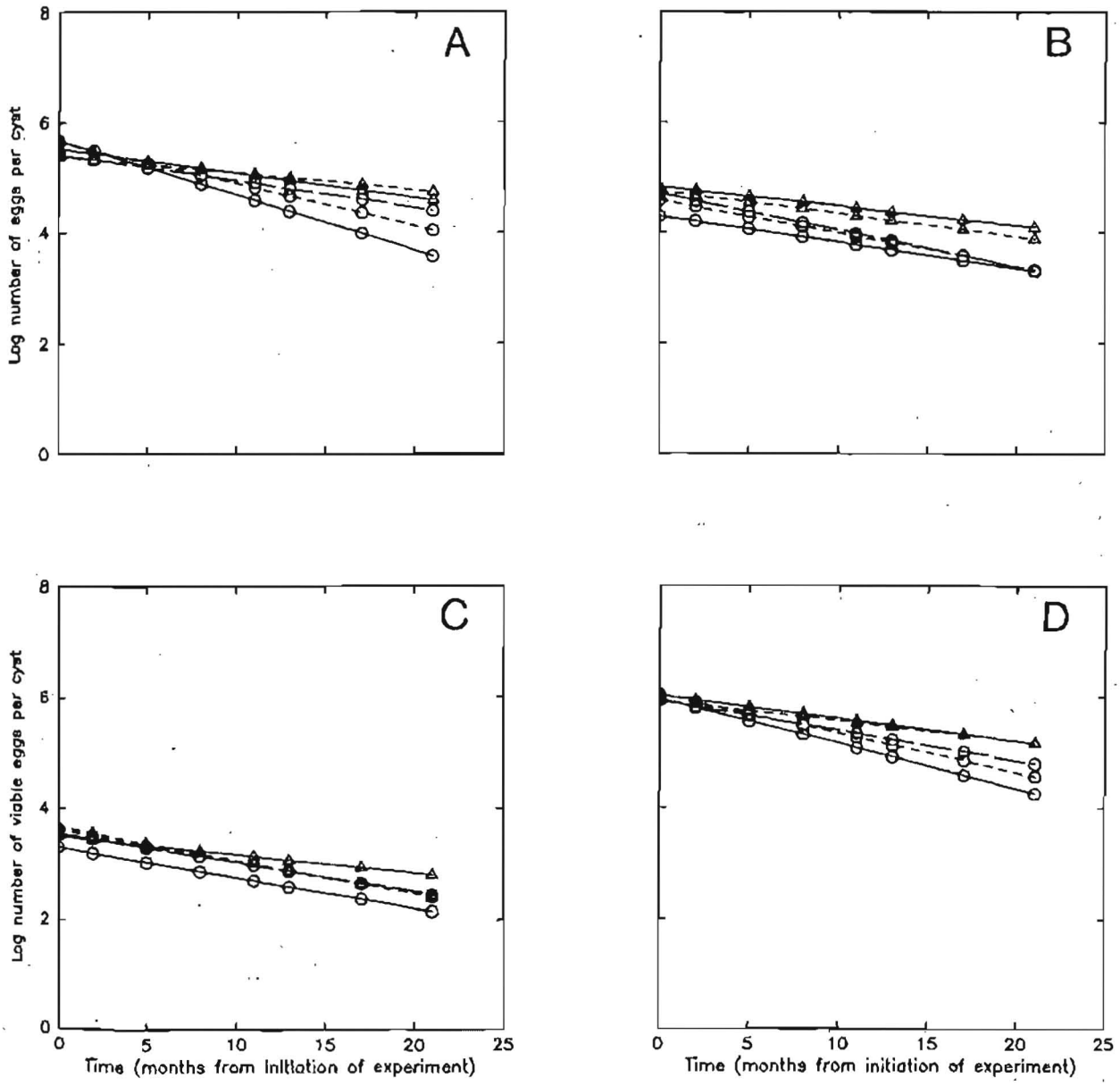

A
B
C
D
Log number of eggs per cyst
Log number of viable eggs per cyst
0
2
4
6
8
0
5
10
15
20
25
Time (months from initiation of experiment)

TABLE 7.3

Regression coefficients (a) and y intercepts (b) for fitted regression lines relating viable eggs/cyst against time for two species and three size classes of cysts at three locations.

Size class		PaS_4 mean	(±SE)	PaC mean	(±SE)	RoS_4 mean	(±SE)	RoC mean	(±SE)	RoO mean	(±SE)
large	a	5.7	(±0.10)	5.5	(±0.09)	6.2	(±0.16)	6.0	(±0.17)	5.6	(±0.17)
	b	-0.04	(±0.01)	-0.03	(±0.01)	-0.09	(±0.01)	-0.07	(±0.01)	-0.05	(±0.01)
medium	a	5.0	(±0.11)	4.9	(±0.21)	4.5	(±0.22)	4.9	(±0.06)	5.0	(±0.23)
	b	-0.03	(±0.01)	-0.04	(±0.01)	-0.05	(±0.01)	-0.06	(±0.01)	-0.06	(±0.02)
small	a	3.6	(±0.14)	4.0	(±0.12)	3.6	(±0.37)	3.9	(±0.15)	3.8	(±0.12)
	b	-0.03	(±0.01)	-0.06	(±0.01)	-0.05	(±0.02)	-0.06	(±0.01)	-0.01	(±0.01)
mean (All)	a	5.1	(±0.09)	4.9	(±0.11)	5.2	(±0.18)	5.3	(±0.12)	5.1	(±0.16)
	b	-0.04	(±0.01)	-0.03	(±0.01)	-0.08	(±0.01)	-0.07	(±0.07)	-0.05	(±0.01)

TABLE 7.4

Comparison of attrition rates between and within species with different sized cysts and grown in different soils.

Species	cyst size		Species	cyst size	Significance (P<0.05)
PaS_4	small	v	RoS_4	small	NS
	medium	v		medium	NS
	large	v		large	**
PaC	small	v	RoC	small	NS
	medium	v		medium	NS
	large	v		large	*
Soil		v			
ROS_4	small	v	RoC	small	NS
	medium	v		medium	NS
	large	v		large	NS
PaS_4	small	v	PaC	small	*
	medium	v		medium	NS
	large	v		large	NS
RoC	small	v	RoO	small	NS
	medlum	v		medium	NS
	large	v		large	NS
Size		v			
Small	RoS_4	v	Medium	RoS	NS
	RoC	v		RoC	NS
	RoO	v		RoO	NS
	PaS_4	v		PaS_4	NS
	PaC	v		PaS	NS
Medium	RoS_4	v	Large	RoS_4	*
	RoC	v		RoC	NS
	RoO	v		RoO	NS
	PaS_4	v		PaS_4	NS
	PaC	v		PaC	NS
Large	RoS_4	v	Small	RoS_4	NS
	RoC	v		RoC	NS
	RoO	v		RoO	NS
	PaS4	v		PaS4	NS
	PaC	v		PaC	*

The decline in egg number in large cysts was significantly faster in Ro_4 than Pa_3 (Figure 7.4.A) but the difference was not significant for other sized cysts (Figure 7.4 B,C).

The higher rate of attrition observed in silts compared with peats for small Pa_3 cysts, and the higher attrition in Canterbury than in the Outram silt loams for large Ro_4 cysts were the only significant soil type effects observed.

Mean annual rates of attrition for each species at each location were calculated using the fitted regression lines (Table 7.3). The number of eggs present after 12 months (Table 7.5) was obtained by solving for y in the equation -

$$\log y = \log a - (\log b)^x$$

where x=12 and division of this value by the initial number of eggs gave percent annual attrition.

TABLE 7.5

Calculated annual percent attrition rate for two species, three cyst sizes and three locations. Calculated from values presented in Table 7.3.

Cyst size	PaS4	PaC	RoS4	RoC	RoO
Small	30.2	51.3	45.1	51.3	45.1
Medium	30.2	38.1	45.1	51.1	51.1
Large	38.0	30.2	66.0	56.8	45.1
Mean (All)	38.1	30.2	61.7	56.8	45.1

Annual attrition rates were consistently higher for Ro_4 than Pa_3, and were lower at Outram than in Canterbury.

7.3.3 Dead eggs

Small numbers of dead eggs were present in cysts at the beginning of an experiment (Table 7.1). However, the number of dead eggs recovered during the experiment tended to decrease with time (Figure 7.5). This was particularly obvious for large cysts, but was highly variable within replicates and between treatments. The data were analysed and the correlation coefficients (r values) (Table 7.6) relating change in egg numbers to time indicated that a high proportion of regressions were not significant ($P>0.05$). The number of dead eggs recovered at any point in time was largely random and not influenced by soil type, species or size class.

TABLE 7.6

Correlation coefficients (r values) relating numbers of dead eggs per cyst with time, The r values were calculated from logarithmically transformed data used in the linear regression equations ($n=4$).

Cyst size	Population codes PaS4	PaC	RoS4	RoC	RoO
Small	0.60	0.03	0.53	0.06	0.03
Medium	0.78*	0.01	0.78*	0.30	0.59
Large	0.76**	0.63	0.24	0.43	0.55
Mean (All)	0.80*	0.52	0.49	0.41	0.60

(* Significant at the 5% level, * * Signifcant at the 1% level)

FIGURE 7.5

Changes in the number of dead eggs (as a percentage of the initial numbers) in two species at three locations for three cyst size classes.

A = PaS4
B = PaC
C = RoS4
D = RoC
E = RoO

circle with short dashed line = large cysts (500-850 micrometres)
triangle with short dashed line = medium cysts (350 micrometres)
diamond with short dashed line = small cyst (250-350 micrometres)
swiss cross with solid line = mean of all sizes

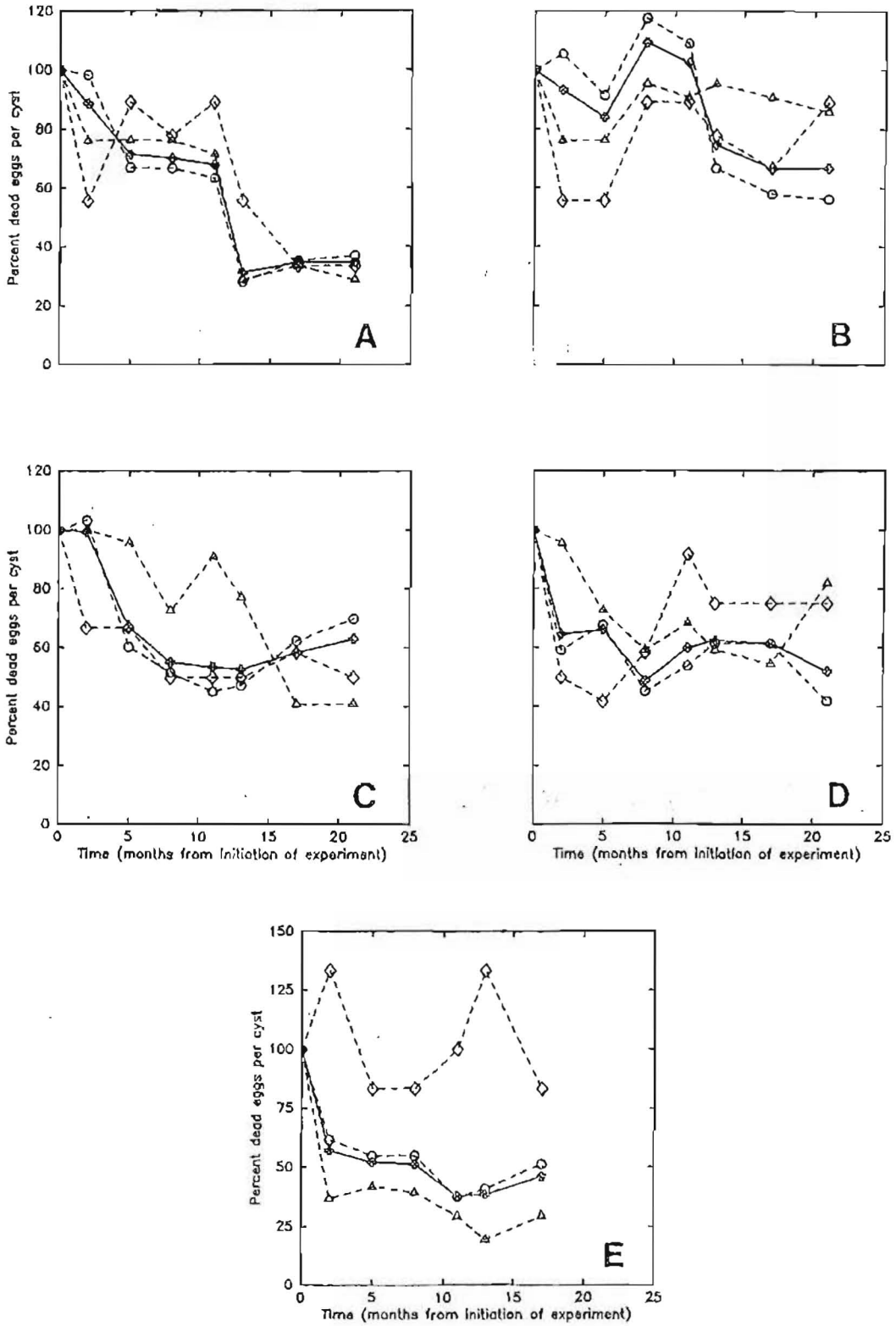
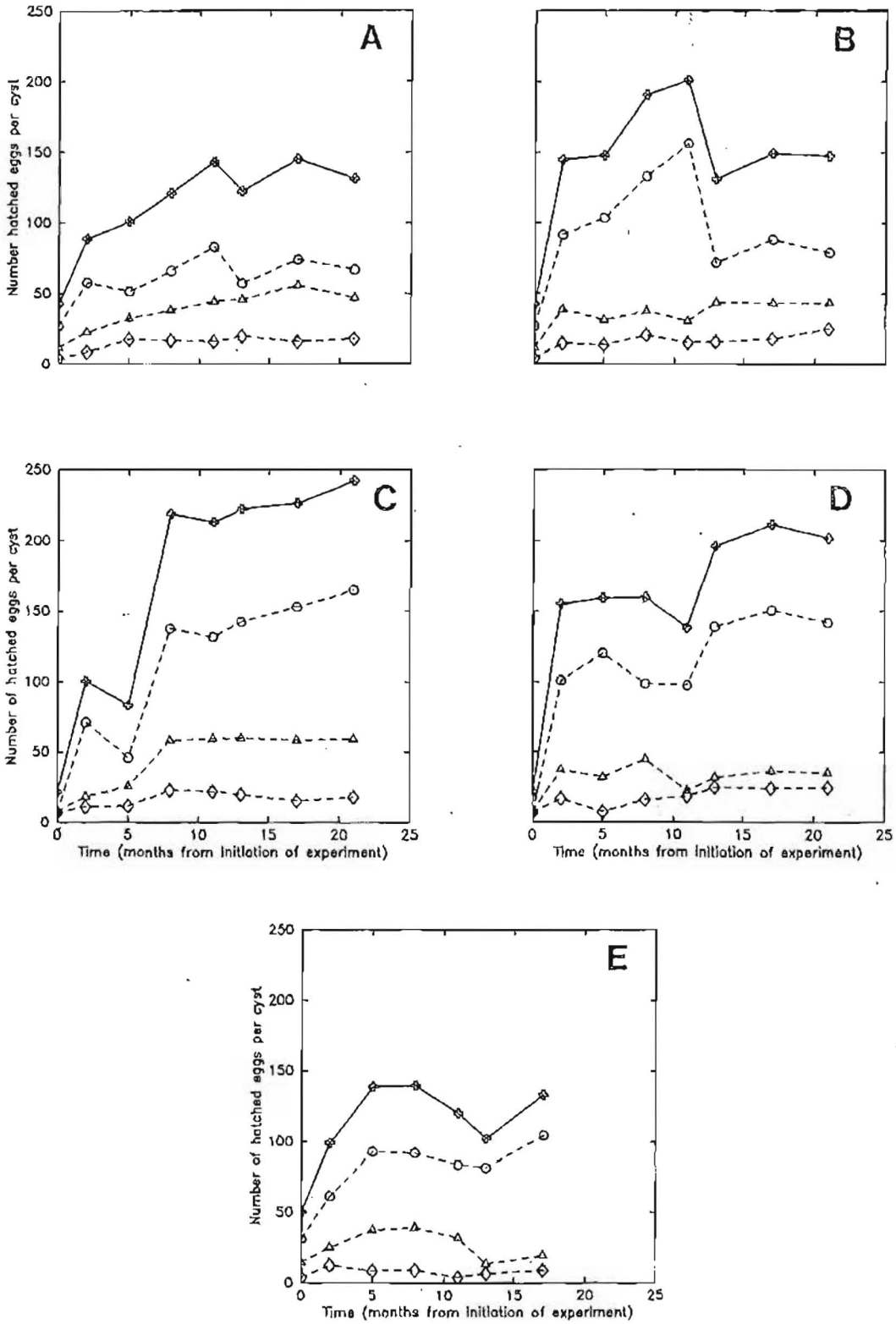

Percent dead eggs per cyst
Time (months from initiation of experiment)
A
B
C
D
E

FIGURE 7.6

Changes in the number of hatched eggs/cyst in two species at three locations for three size classes of cyst.

A = PaS4
B = PaC
C = RoS4
D = RoC
E = RoO

circle with short dashed line = large cysts (500-850 micrometre)
triangle with short dashed line = medium cysts (350-500 micrometre)
diamond with short dashed line = small cysts (250-350 micrometre)
swiss cross with solid line = mean of all sizes


A
B
C
D
E
Number hatched eggs per cyst
Number of hatched eggs per cyst
Time (months from initiation of experiment)
0
50
100
150
200
250
0
5
10
15
20
25

7.3.4 Hatched eggs

The number of egg shells present in cysts increased with time (Figure 7.6) and their increase followed a generally asymptotic curve. In the first 12 months the number of egg shells increased but after this time they began to level off. Ro in peat was an exception since little increase in egg shell numbers was found. Not surprisingly, the pattern of increasing egg shell numbers in the first 12 months was essentially the reciprocal of the pattern for viable egg decline shown in Figure 7.3. After 12 months, this pattern was disrupted as the number of egg shells remained more or less constant although a decline in viable eggs continued.

7.3.5 Soil temperature and moisture

The mean soil temperature and soil moisture for all three study areas for the duration of the study are presented in Appendix VII and Appendix VIII.

7.4 DISCUSSION

Mature cysts free in the soil encounter a different set of survival problems from those encountered during development in a host root. In soil, the cyst must be sufficently insensitive to the environment to survive for an extended period yet be able to respond to the stimulatory effects of a suitable host plant. Factors that stimulate potato cyst nematode eggs to hatch in the presence of a host have been discussed extensively and reviewed by Shepherd (1962b) and Clark and Perry (1977). However, little detailed study has been attempted on the fate of cyst contents in a field situation in the absence of a host.

In the present study I showed that there was no reduction in the number of cysts present in the soil in the first two years but that the number of viable eggs declined with time. Loss of viable eggs was caused by hatching rather than death within the cyst and Ro had a more rapid rate of attrition than Pa.

Egg hatching in the absence of a host can be affected by diapause or dormancy (Evans and Perry, 1976; Shepherd, 1962b; Ellenby and Smith, 1967) and can result in a spring flush of hatching. This is not a universal phenomenon, however, and was not observed by Rode (1971) or Wood and Foot (pers. comm.)

Attrition rates observed in the present study were log-linear for both species and cyst size. A dormancy period was not found. Jones and Kempton (1978) logarithmically transformed the arithmetic results of Cooper (1954) to demonstrate a similar constant rate of population

decrease, which had not been immediately apparent when plotted on a linear scale by Cooper (1954).

Cole and Howard (1959) also plotted percentage decrease in egg numbers over time but failed to recognise the constant rate of decline because it was plotted on a linear scale. Logarithmic transformation of their data showed a similar constant rate of population decline. It is interesting to note that published figures from Cole and Howard (1962) do not show a constant rate of attrition, as the percentage loss in the first year was much higher than in the following year. Such observed variation in results of attrition studies carried out on a greater time base than the present study suggests that although a constant rate of decline can be demonstrated by intensive sampling over a short time, long term attrition may not necessarily conform to the same pattern and to extrapolate beyond the data points is ill advised.

The decline in the number of dead eggs in cysts over the experimental period was largely random but occurred at a much lower rate than viable egg losses.

An increase in the number of egg shells was also observed. This was the result of egg hatching and was the reciprocal of the decline in viable eggs. This relationship broke down after approximately 12 months when egg shell numbers in samples became more-or-less constant whereas the number of viable eggs continued to decline. I conclude from this that some egg shells had already begun to decompose at this time and so were not found in later samples.

Significant differences in the overall attrition of viable eggs were found between Ro_4 and Pa_3; these differences were independent of location (Table 7.4). Attrition rates tended to be higher in the silt soils of S4 than in the peat soil of Cranford St. Ro_4 in the silt loams of Outram occupied an intermediate position. Attrition rates calculated for the three size classes of cysts were not significantly different.

Wallace (1955, 1956, 1958, 1959, 1963) concluded that aeration was the most important soil factor affecting the emergence of larvae from cysts but he also considered that the structure and composition of the soil was important. This is because these factors influence the degree of soil aeration and subsequent larval emergence.

In my study, differences in emergence occurred in the three soil types used, and an examination of their physical characteristics suggests a possible explanation for this.

The greatest loss in viable eggs occurred in the Canterbury silt soils which exhibited a well developed structure and 'crumb'. Wallace considered soil structure to be, "a vague term but I define it

here as the arrangement of soil particles, the word particle meaning not only the individual elements such as sand, silt and clay, but also the units formed by an aggregation of these smaller fractions, commonly termed crumbs". The crumbs in S4 soil had large interstitial pores which allowed extensive soil aeration. Soil moisture (Appendix VIII) at S4 was above soil capacity during winter but drained readily in spring and summer. Regular wetting and drying ensured full aeration and at the same time the soil was subjected to a seasonal heating and cooling regime (Appendix VII). According to Bishop (1955) these conditions produce optimal larval emergence.

The level of oxygen consumption within a soil varies between soil types, and is lowest in soils containing large sand particles and low organic content (Russell, 1950; Wallace, 1956). This type of soil occurs at S4. In contrast, the Outram soils although highly mineralised are made up of fine particles and are almost structureless with small interstitial pores which are further reduced by the presence of clay particles.

One effect of the clay component would be to increase the oxygen consumption of the soil as indicated by the work of Wallace (1956). Soil moisture at Outram never reached field capacity (Appendix VIII) and did not exhibit a marked seasonal fluctuation. This probably reflects the water holding capacity of the clay particles especially as the seasonal soil temperature regime was similar to that of S4.

Finally, the peat soils of Cranford St. (where the lowest attrition rates were found) can be considered to be incompletely drained soils where full aeration is seldom achieved.

Although raw peat soils are made up of large pieces of undecomposed organic particles which allow good aeration when drained, this is not the case in cultivated peats such as Cranford St. where organic material has been broken down into small particles and in extreme cases is powder like. This results in a largely structureless top soil with very small pore spaces. Drying of the soil is restricted to the top layers and the rest of the soil profile becomes progressively wetter with depth.

Soil moisture samples taken from Cranford St. (Appendix VIII) showed strong seasonal fluctuations, but the moisture content never fell below 45% (oven dry weight) which is roughly twice that of the other soil types examined. Soil temperature fluctuations were similar to those recorded at S4 except that summer temperatures were higher.

In addition to having relatively poor aeration characteristics, peat soils have a high oxygen consumption which would further restrict the amount of oxygen available to the dormant cyst (Wallace 1963).

7.5 SUMMARY

1. Attrition rates were higher in silt than in peat soils and were higher in Ro_4 than Pa_3.

2. Cyst size did not signficantly influence the rate of attrition.

3. Attrition rates for both species were log-linear over the duration of the experiment and were primarily the result of emergence of hatched larvae not death of eggs.

4. Reduction in dead egg numbers was largely random and the result of decomposition processes. Species and cyst size had no apparent influence.

5. Empty egg shells accumulated following initial hatching but after 12 months the number of egg shells present leveled off.

6. Highest annual attrition rates occurred in soils which were free draining and had good structure. The presence of high organic matter or high proportions of clay particles reduced the attrition rate.

CHAPTER 8

CONCLUDING REVIEW

New Zealand is a primary producing country and depends largely on export markets for its economic survival.

Traditionally, the United Kingdom has been our principal market and low cost efficient production coupled with an assured market have offset the considerable cost of supplying a market halfway round the world. With the advent of the European Economic Community (EEC) this market has been reduced seriously and is no longer assured. As a result, New Zealand has been forced to diversify both its markets and produce. Distance from markets is still a distinct disadvantage but this very isolation has been of great virtue in keeping New Zealand relatively free from other countries' pests and diseases. As a result, New Zealand enjoys a good reputation which has enabled us to maintain a high level of confidence in meeting the export requirements of markets.

A well developed quarantine service helps maintain this freedom from pests and diseases and at the same time is responsible for the restriction, reduction and control of any pest present in New Zealand. Such vigilance is frequently challenged by those who would argue that it is better to allow every pest into every country and then implement policies based on the premise:- "It's everywhere so let's live with it". This approach, while theoretically straightforward, ignores the fact that it is easier and cheaper to restrict and control a pest at the colonization phase when distribution is limited than to manage a pest when it has spread over a wide range of sites. Also, not every pest has the same capacity to colonize, establish, multiply and spread.

Significantly, most proponents of the "live with it" philosophy are microbiologists who rightly recognise there is very little that can be done to restrict the spread of spores and other such airborne micropropagules. However to extend this argument to invertebrate pests such as nematodes cannot be sustained. Containment of such pests is a worthwhile pursuit as theoretically it is possible to stop colonisation of a pest, and certainly it is practical to limit the rate and spread of a pest by quarantine measures. This is especially so if its original site of infestation is apparently limited and the pest does not move quickly. Such action although causing localised hardship is likely to protect the greater part of the country for a longer period.

One cannot argue that quarantine will guarantee that an area currently free of a pest will stay free, but it certainly "buys time" in

which the farming sector saves money and the scientific community can develop suitable management practices.

In addition to its practical aspects, the presence of internal quarantine activity in itself establishes confidence in our primary industries on the world scene.

It was against this philosophical backdrop that potato cyst nematode (PCN) was discovered in 1972. Because of its recognised impact on potato production and its well documented international trade consequences, PCN was treated by the Ministry of Agriculture and Fisheries as an outbreak situation. An immediate survey of the affected area was undertaken, all infestations were fumigated at government expense and the land was retired from solanaceous cropping.

This course of action immediately reduced the known infestations and the risk of greater spread from these areas. Subseqently, a national survey was undertaken to establish the extent of the problem. Three distinct areas of commercial production were found to be infested but they did not include the bulk of New Zealand's potato cropping areas. Because of its apparently limited distribution, a policy was formulated, the stated objectives of which were to contain, control and reduce PCN populations in New Zealand.

To achieve these objectives a large number of specific questions had to be answered. Thus, research units were established by DSIR in both Islands to supply information and advice to MAF and to assist in the formulation of management strategies for PCN.

The present study forms part of the reseach program. Its specific objectives were to study the biology of the pest in the South Island and compare the ecology of the two species, G. rostochiensis and G. pallida. Although routine in a number of aspects the regional approach was essential in this case as information already obtained at Pukekohe was unlikely to be applicable to South Island situations.

The results of this study have been presented in the previous chapters and in this review are considered in the same order.

On a national level, yield losses observed in the present study can be compared with those obtained by Wood and Foot (1977b) and Foot et al. (1980) at Pukekohe. Wood and Foot (1977b) established that loss in yield became significant at a nematode egg density of approximately 20 eggs/ml. This response threshold is comparable with that observed in the present study. Wood and Foot (1977b) in New Zealand and also Seinhorst (1967a) and Oostenbrink (1966) working in Holland noted that low egg levels had a stimulating effect on plant growth, but this was not observed in the present study. Yield losses are related to initial

density and typically are described by a sigmoid curve (Lownsberry and Peters, 1955; Jones, 1956; Hesling, 1957; Hoestra and Oostenbrink, 1962; Seinhorst, 1965, 1970; Jones et al., 1967; Seinhorst and Den Ouden, 1971; Jones and Kempton, 1978; Stelter et al., 1980, and Foot et al., 1980).

Maximum yield loss in the present study (90% of control) occurred at an initial egg density of approximately 150 eggs/ml. This was much higher than at Pukekohe where maximal yield loss amounted to about 50% and resulted from an initial egg density of 60 eggs/ml. However it is similar to results obtained by Seinhorst and Den Ouden (1971) who showed that a significant loss in yield occurred at about 20 eggs/g of soil and maximum loss (80%) occurred at an initial pre-plant density of 300-800 eggs/ml of soil. Population equilibrium of both Ro and Pa in Canterbury was similar (a mean of 312 eggs/ml of soil) and again was higher than at Pukekohe (100 eggs/ml). However, in a British population studied by Jones and Parrott (1969) equilibrium occurred at 59 eggs/ml of soil and Seinhorst and Den Ouden (1971) in Holland recorded an equilibrium density of 100 eggs/g soil.

There was also a large difference in the maximum multiplication ability of the Canterbury and Pukekohe populations; similar egg densities (less than 1 egg/ml) produced multiplication factors of 93x and 25x, respectively. The Pukekohe factor compares well with those observed in Holland (x22, Seinhorst and Den Ouden, 1971) and Ireland (x22 Winslow, 1972). Fecundity (eggs/cyst) in the study of Seinhorst and Den Ouden (1971) was about 100 eggs/cyst and initial egg density had little effect. The English population studied by Evans (1969) had a fecundity of 100-150 eggs/cyst which although not greatly different from the Dutch population was much lower than the values of about 200 eggs/cyst for Pa and Ro in Canterbury.

Foot (1978b) found that at Pukekohe (Pa_2) fecundity was between 160-240 eggs/cyst depending on planting date and that environmental factors had a great influence on fecundity. She demonstrated this effect by rearing nematodes in a controlled environment and showed that under optimal conditions (17.5°C) fecundity of both species increased to 400-500 eggs/cyst. Thus it appears that in Canterbury PCN has established in a favourable environment and high fecundity and multiplication rates results in both rapid population increase and extensive host debilitation.

The life cycle of both species was studied by the construction of life tables and results of the present age specific life study can be compared directly with those of Foot (1978b) at Pukekohe. However,

there is an absence of other comparable works (Jones and Kempton, 1978). Foot's (1978b) study dealt specifically with G. pallida (Pa_2) whereas in the present study both Pa_3 and Ro_4 were considered. The spring planting period at Pukekohe corresponds to the early planting period in Canterbury.

A comparison of data obtained from Pukekohe and Canterbury shows that the pattern of mortality for all life styles was similar for both populations except for life style C (in the root) which had a higher mortality in Canterbury. Duration of each life style was also very similar except for life style D (adult) at Pukekohe which took 41 days compared with 29 days in Canterbury.

Chitwood and Buhrer (1946) working with G. rostochiensis measured the interval of each juvenile instar and stated that generation time (i.e. the duration between embryonated egg and embryonated egg) was between 38 and 48 days as observed in this study and by Foot (1978b). The time between planting date and hatching was not mentioned by Chitwood and Buhrer (1946) but a large difference in the length of this period was found between the Pukekohe and Canterbury populations. The latter hatched soon after planting (7-10 days) whereas the Pukekohe population did not respond for at least 34 days after planting.

A G. rostochiensis population in Cyprus (Phillis, 1980) had a slow hatching response similar to that observed at Pukekohe, but duration of the larval stages was inversely related to soil temperature. Evans (1969) observed a similar inverse relationship. This is consistent with the results of the Canterbury experiments and contrasts with the Pukekohe population which was less responsive to soil temperature changes. Development times of Ro generally were shorter than Pa, a finding that is consistent with that of McKenna and Winslow (1972).

Sex ratios also differed in Canterbury and Pukekohe with males better represented in the latter. Both Ro and Pa populations in Canterbury had fairly similar sex ratios throughout the season but increased with time which is in direct contrast to the findings of Foot (1978b) who observed a decrease in sex ratios with time.

Effective population multiplication (number of live eggs in inoculum divided by total number of new eggs produced) was generally highest in spring plantings at both locations with mean multiplicative values of 15.6 and 49.6 obtained at Pukekohe and in Canterbury respectively. It seems likely that the between population difference is brought about by edaphic factors (Foot 1978b).

In Canterbury, as elsewhere (Jones, 1950; Phills, 1980), an increase in soil temperature during the growth period decreased the duration of each life style whereas at Pukekohe the population were much less responsive and soil temperature influenced larval mortality rather than duration of life cycle. An increase in soil temperature reduced effective multiplication of both Ro and Pa in Canterbury and Pa in Pukekohe, as has been observed by Ferris and Mai (1956). The low multiplication observed in the Outram population was related to low soil temperature in the early stage of the life cycle causing high life style B mortality.

G. pallida populations in Canterbury appeared to be more sensitive to increases in soil temperature than those of Ro, and their multiplication rates decreased more rapidly at higher temperatures. Stone and Webley (1975) published a similar finding and Foot (1978a) showed that Ro could maintain a higher multiplication rate at higher temperatures than Pa whereas the multiplication of Pa was higher at lower temperatures. She found that the optimum temperature for the development of both species was 15-20^{o}C.

In my study the life style in which greatest mortality occurred was life style B. This is consistent with Foot's (1978b) findings. Survival curves calculated for both Ro_4 and Pa_3 in Canterbury and Pa_2 at Pukekohe were very similar.

Cropping patterns at Outram were similar to those of winter plantings at Pukekohe as both were planted at a low soil termperature. The populations had an extended development time and after 96 and 100 days respectively, populations at Pukekohe and Outram had reached only the immature, white female stage. Harvesting at this time resulted in low cyst fecundity. Effective multiplication was also low.

When the population was able to develop to full maturity (at Outram after 150 days) the multiplication rate and fecundity increased substantially. This was the direct result of increased cyst size, and reduced egg mortality within the cyst (Brande and D' Herde, 1964) and Mugnlery (1978) also noted an increase in cyst size and fecundity if the nematode had a full development time.

A significant difference in the time taken for larvae to hatch from the cyst was observed between Outram and Pukekohe populations grown under similar soil temperature regimes. The latter did not respond to root exudate for two-three weeks whereas Outram larvae hatched within 10

days. Once stimulated, the bulk of the L_2 larve at Pukekohe rapidly hatched whereas at Outram hatching continued for approximately 61 days without a pronounced peak. Very high mortality within the soil was associated with this extended L_2 phase.

The ability of Outram nematodes to hatch at lower temperatures (mean 9.4°C) is typical of populations associated with early planting areas, and has been recorded elsewhere by Chitwood and Buhrer (1946); Grainger (1964); Brande and D'Herde (1964); Ellenby and Smith (1975); Mugniery (1976), and Hominick (1979).

No mass invasion of host plants by L_2 larvae was observed at Outram but rather there was gradual and extended colonisation. Similarly, Hominick (1979) reported an extended hatching period in Ayrshire (Scotland) and noted that the proportion of unhatched eggs was high (30-40%). In contrast, only about 10% of eggs failed to hatch at Outram.

Despite high mortality and interrupted development in the early cropping areas, some nematodes do reproduced successfully. This led Ellenby and Smith (1975) to postulate that planting at low soil temperatures and early harvesting selects for nematodes with an ability to hatch at low temperatures and that only they complete development before the early harvest.

There is now ample evidence substantiating the concept of low temperature hatching adaptation, but evidence of ability to complete a life cycle before early harvest is not as well documented. Grainger (1964) stated that immature females dislodged from roots at harvest make little contribution to the next generation, but my study at Outram showed that they made the major contribution to the next generation, and were capable of maturing in the absence of a host plant. Therefore, if any selection for development were to occur it should be in this section of the population. In addition to this, a proportion of the population which had not fallen off the root at harvest matured on the discarded root tissue and it can be argued that this component of the population is selected for late development. Both components respond in the same way to subsequent early potato plantings.

The presence of selfsets (ground keepers) further complicates the picture as the early formed cysts (free in the soil) have time to mature and respond to the presence of selfsets. However, their multiplication is low. The late developing cysts (in root tissue) do not respond and although the carry over component in old cyst source is stimulated to hatch it suffers very high mortality and has low multiplication.

Grainger (1964) observed a similar response in the Ayrshire population when grown on selfsets.

At Outram, a range of selection pressures apparently act on different components within the same population, (all of which have the capacity to interbreed), and it seems unlikely that a strain of rapidly developing nematodes could occur naturally.

Interspecific interactions between the two nematode species present in the same host were demonstrated in the Canterbury environment. Ro had a higher multiplication rate than Pa and this resulted in reduced numbers of Pa in mixed populations. This is consistent with experimental results obtained by Parrott and Berry (1978) but conflicts with the findings of some earlier work by Parrott *et al.* (1975). However, interpretation of field observations made by Cole and Howard (1962) and Huijsman (1961) tend to support the case of Ro dominance in a mixture.

Although *G. pallida* was not recognised as a distinct species at the time (1961-62) the rapid decrease in Ro density, (with the repeated use of Ro resistant potatoes) followed by a levelling off and subsequent increase in numbers (in this case a Pa population) demonstrated the presence of a community which had contained a dominant species and a second less successful species (Huijsman, 1961; Cole and Howard, 1962). This less competitive species while coexisting, could only increase when absolute numbers of the dominant species were reduced. The establishment of dominance between Ro and Pa was largely the result of interactions during hatching, and penetration of the host and their different responses to environmental factors.

Kinlock and Allan (1972) who worked with two species of *Meloidogyne* (*hapla* and *javanica*) found that *M. javanica* was usually dominant in a mixture and this dominance was enhanced when initial density of *M. javanica* was high. The modifying effect of environmental pressures was also noticed as *M. hapla* was dominant at lower temperatures when it developed more rapidly.

In the present study, similar replacement of Pa by Ro was found under a range of Pa:Ro ratios. However, when Pa was less abundant in the initial mixture, it was able to maintain its representation in the mixture.

A much greater body of literature is available on interactions between species in different genera than on congeneric species. (Alongi and Tietjen, 1980; Chapman, 1979; Estores and Chen, 1972; Freckman and Chapman, 1972; Gay and Bird, 1973; Johnson and Nusbaum, 1970; Miller and Wihrheim, 1968; Sikora *et al.*, 1979, 1979; Turner and Chapman,

1972; Welscher, 1974). Most studies demonstrated some form of interaction and often this resulted in dominance of one species. Miller's (1970) work on a Heterodera tabacum and Pratylenchus penetrans is a good example.

Attrition rates of the two species also differ in the absence of a stimulating host, both Pa and Ro lose viable larvae but I found this was greater in Ro than Pa. Observed attrition rates (Ro 58%, Pa 34%) were lower than those reported by Foot et al. (1980) for Pa from Pukekohe (70%) and comparable with those found in European situations where seasons are more clearly defined (Fenwick, 1950; Goffart, 1952; Oostenbrink, 1952; Jones, 1956; Hesling, 1958).

Cyst size did not have a marked influence on attrition rate and most attrition was the result of larval hatch rather than mortality within the cyst. Shepherd (1961) also found this to be the case in a population of H. goettingiana.

Soil type also influenced the rate of attrition which was greater in open friable soil (S4) than in organic peat (Cranford St.) or fine silt loams (Outram). This is in line with the findings of Wallace (1955, 1956a, 1958, 1959, 1963) who attributed soil associated hatching effects to differences in the aeration capacity of the soils.

SUMMARY

The major findings of this study are:-

1. The population biology of *G. rostochiensis* and *G. pallida* differ with *G. rostochiensis* being a more effective parasite than *G. pallida*.

2. Premature removal of the host plant does not result in the death of immature cysts as dislodged cysts can complete their development in the absence of the host.

3. Within the life cycle, mortality is greatest in the larval stage which is free in the soil (life style B) and is affected by soil temperature and soil type.

4. *G. rostochiensis* is competitively superior to *G.pallida* in most situations.

5. Loss in viability within the dormant cyst is the result of active egg hatching rather than within-cyst mortality and is greater in *G. rostochiensis* than *G. pallida*.

6. The rate of attrition is influenced by soil type. Open, well aerated soils produce the highest attrition rates.

In summary, this study provides basic biological information on potato cyst nematode in the South Island of New Zealand and in combination with advances in chemical control and in the breeding of resistant potato cultivars has enabled the establishment of a largely successful control and management program for this pest.

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APPENDIX I

Detailed soil profiles of S4 Lincoln.

Eyre Series. Raeside and Rennie (1974)

Eyre soils range from well drained shallow silt loam to excessively drained stony sandy loam. The thickness of fine sediment over gravels is less than 45 cm and in many places less than 25 cm, and topsoils are stony in many places. These soils have formed on the coarse gravels of an ancient flood plain. They occur both on surfaces slightly elevated above the surrounding deep Templeton soils and in ancient watercourses below the general level of surrounding land. The surface is mostly undulating to rolling and includes braided channels, dunes and terrace scarps with some flat terrace treads. Where the surface is uneven, stony soils tend to border the sides of old stream channels and shallow soils occupy the channel floors.

Top soils are mainly between 15 and 25 cm thick and consist of silt loam and sandy loam with varying stone content. Organic matter levels are lower than those in Templeton soils and structures are more weakly developed.

Eyre silt loam, shallow phase. Mostly as a complex with the very shallow or stony Eyre soils. It consists of 15 to 45 cm silt loam, over gravels with a sand matrix in the deeper soils, or a silt loam or sandy loam matrix in the shallower soils. In the shallower soils, the uppermost gravels are firmly packed with silt loam or sandy loam and the sandy gravels below are moderately cemented with brown colloid. Topsoils and upper subsoils are friable in most places. A profile is:

0-200 mm very dark greyish brown silt loam; friable; strongly developed fine and medium nut and cast granular structure; distinct boundary,

200-230 mm brown silt loam; friable; moderately developed fine nut and cast granular structure; distinct boundary,

230 mm gravels packed with silt in the top 5 cm, with sand below.

APPENDIX II

Detailed soil profiles of Cranford Street, Marshlands.

Waimairi Series, Raeside and Rennie (1974).

Waimairi peaty loam - south-west of Halswell and in the Marshlands area. It consists of 25 to 50 cm of mellow peaty loam over alluvium. Where the organic matter is well decomposed it forms black or dark reddish brown topsoils, but where it is more fibrous the topsoils are browner. Before the peats were drained the surface was almost flat but after the water table had been lowered by drainage, the peat shrank and consolidated exposing tree stumps in places and the surface became uneven. To some extent, intensive cultivation has again smoothed the surface. Where over-drained the peaty loam dries out excessively in summer and does not re-wet readily in autumn, thus the risk of wind erosion is increased. A profile is:

0 - 300 mm dark brown peaty loam; friable; moderately developed medium and fine granular with some crumb structure; very many roots; indistinct boundary.

300 - 310 mm dark brown peaty loam; many very dark brown worm casts throughout; friable; moderately developed medium and fine granular structure; many roots; undecomposed wood fragments; indistinct boundary,

310 - 318 mm dark brown peaty loam; friable; medium and fine granular structure; much undecomposed wood fragments; distinct boundary,

318 - 330 mm dark greyish brown silt loam; orange brown stains along root channels; friable; fine granular structure; abundant undecomposed wood; distinct boundary.

330 on greenish grey heavy silt loam; many diffuse pale olive brown mottles; very firm; massive; much undecomposed wood.

Analyses of the peaty loam show very high total nitrogen, cation-exchange capacities, base saturation, calcium and magnesium with high levels of potassium.

The mellow topsoils are very friable and well supplied with major plant nutrients. Waimairi peaty loam is of high natural productivity.

APPENDIX III

Detailed soil profile of Outram.

Clutha silt loam, Beecroft (pers. comm.)

0 - 150 mm very dark greyish brown silt loam; weakly developed fine and medium nut structure; moderately weak strength; brittle deformation; slightly sticky; moderately plastic; firm penetration; 2-3% fine faint dark reddish brown mottles; many fine roots; indistinct smooth boundary;

150 - 280 mm very dark greyish brown silt loam; weakly developed medium blocky structure; moderately firm strength; brittle deformation; slightly sticky; moderately plastic; firm penetration; 2-3% fine faint dark reddish brown mottles; few fine roots; distinct irregular boundary;

280 - 800 mm light olive brown silt loam; weakly developed coarse prismatic structure; moderately weak strength; brittle deformation; slightly sticky; moderately plastic; firm penetration; 2% very fine faint dark yellowish brown mottles; few fine roots; sharp wavy boundary;

APPENDIX IV

Mean numbers of larval nematodes extracted from 5g of stained potato roots using different methods.

Method	n	Larval Stages				Total
		L_2	L_3	L_4	L_4	
Hand dissection	5	71.4ab	80.0ab	25.4ab	13.0a	189.8a
60 sec. maceration	5	40.2c	64.0b	17.6b	6.0	127.8
3x20 sec. maceration and sieving; (25ml counted)	5	79.ab	96.8ab	24.6ab	11.0a	211.4a
Aggregated tissue sample; (25ml counted)	5	53.bc	92.2a	28.2a	10.8a	184.8a
Aggregated tissue resample (12.5ml counted) (Corrected to 25ml)	5	85.a	91.8a	28.2a	10.6a	215.6a

For each column, figures with letters in common are not significantly different at the 5% level.

n = number of replicate 5g samples.

APPENDIX V

Mean number and weight of table and seed size tubers produced for three years in Pa infested plots and uninfested control plots. (A, B, C and D = microplot at different densities - Chapter 3).

	CONTROL mean	(±SE)	INFESTED mean	(±SE)	CONTROL mean	(±SE)	INFESTED mean	(± SE)
			Table No.				Table weight (kg)	
1979								
A	141.0	(±6.1)	145.0	(±9.0)	24.5	(±1.6)	23.3	(±2.2)
B	110.0	(±1.8)	118.0	(±8.3)	18.5	(±0.3)	19.3	(±9.9)
C	131.0	(±9.5)	94.0	(±6.1)	18.2	(±1.3)	13.5	(±9.0)
D	110.5	(±3.2)	94.0	(±6.1)	18.2	(±1.3)	13.5	(±0.33)
			Seed No.				Seed wgt. (kg)	
A	290.0	(±37.0)	224.5	(±20.5)	8.7	(±1.0)	7.6	(±0.7)
B	382.0	(±40.4),	236.0	(±27.5)	10.2	(±0.45)	7.4	(±0.65)
C	287.0	(±16.5)	24.0	(±16.4)	9.3	(±0.45)	7.2	(±0.60)
D	320.0	(±30.3)	243.0	(±15.4)	9.1	(±0.85)	6.9	(±0.6)
			Total No.				Total wgt. (kg)	
A	431.0	(±32.0)	39.6	(±15.5)	33.2	(±1.0)	30.9	(±1.6)
B	492.0	(±83.8)	354.0	(±65.4)	28.7	(±0.7)	26.7	(±2.1)
C	4 8.0	(±11.4)	307.8	(±82.6)	30.7	(±1.6)	17.2	(±1.5)
D	431.0	(±27.4)	33.7	(±64.4)	27.4	(±1.5)	25.4	(±2.1)

APPENDIX V (cont'd)

	Table No.				Table wgt. (kg)			
1980								
A	134.8	(±11.0)	82.0	(±3.5)	17.7	(±1.3)	9.7	(±9.3)
B	116.3	(±5.2)	23.5	(±7.3)	15.2	(±1.2)	2.2	(±0.25)
C	103.0	(±7.3)	7.0	(±2.6)	12.7	(±0.95)	0.58	(±0.25)
D	92.5	(±5.3)	3.7	(±0.53)	11.8	(±0.59)	0.30	(±0.09)
	Seed No.				Seed wgt. (kg)			
A	158.8	(±11.1)	125.3	(±11.1)	5.7	(±0.95)	4.5	(±0.3)
B	139.8	(± 9.5)	86.8	(±14.5)	4.8	(±1.57)	2.8	(±0.38)
C	132.0	(± 8.4)	47.0	(±6.8)	4.7	(±0.95)	1.4	(±0.15)
D	156.0	(± 8.5)	22.5	(±5.0)	4.8	(±0.6)	0.6	(±0.2)
	Total No.				Total wgt. (kg)			
A	292.5	(±10.1)	207.3	(± 8.7)	23.5	(±18.2)	1.2	(±1.5)
B	256.0	(±8.2)	110.3	(±20.5)	20.1	(±19.1)	5.0	(±0.9)
C	235.0	(±8.0)	54.0	(± 9.2)	17.5	(±17.3)	2.0	(±0.41)
D	248.8	(±11.3)	26.3	(± 4.5)	16.7	(±15.5)	0.9	(±0.14)
1981								
	Table No.				Table wgt. (kg)			
	41.8	(±11.0)	6.3	(±1.4)	4.8	(±0.2)	0.7	(±0.10)
	Seed No.				Seed wgt. (kg)			
	110.8	(± 7.1)	74.7	(±7.1)	4.7	(±0.9)	3.0	(±0.25)
	Total No.				Total wgt. (kg)			
	152.5	(±17.7)	81.0	(±12.1)	9.5	(±1.5)	3.7	(±0.10)

APPENDIX VI

Mean number and weight of table and seed size tubers produced for three years in Ro infested plots and in uninfested control plots. (A, B, C, and D = microplot at different densities - Chapter 3).

	Control mean	(±SE)	Infested mean	(±SE)	Control mean	(±SE)	Infested mean	(±SE)
	Table No.				Table wgt. (kg)			
1979								
A	130.0	(± 9.3)	117.0	(±11.3)	20.4	(±3.2)	20.6	(±4.8)
B	110.3	(±10.0)	96.3	(±7.0)	17.7	(±3.2)	15.2	(±3.4)
C	125.8	(±73.0)	57.5	(±8.8)	20.6	(±1.6)	8.4	(±1.8)
D	97.8	(± 9.5)	47.5	(±5.8)	15.8	(±2.3)	7.1	(±1.0)
	Seed No.				Seed wgt. (kg)			
A	284.3	(±29.5)	311.0	(±13.4)	9.9	(±1.7)	8.8	(±0.8)
B	387.3	(±21.9)	283.8	(±24.4)	10.5	(±0.62)	7.9	(±0.58)
C	307.3	(±21.5)	244.5	(±28.8)	9.2	(±0.15)	7.3	(±0.70)
D	392.8	(±39.5)	287.5	(±17.5)	9.7	(±0.7)	7.7	(±0.50)
	Total No.				Total wgt. (kg)			
A	414.0	(±34.5)	428.0	(±12.0)	30.3	(±2.0)	29.4	(±2.3)
B	498.0	(±24.4)	380.0	(±20.0)	28.2	(±2.4)	23.2	(±1.6)
C	433.0	(±20.2)	302.0	(±36.0)	29.8	(±2.5)	15.7	(±2.4)
D	490.5	(±33.7)	335.0	(±19.5)	25.2	(±2.0)	14.8	(±0.8)

APPENDIX VI (Cont'd)

	Table No.				Table wgt. (kg)			
1980								
A	119.5	(±10.5	74.0	(±25.5)	14.2	(±1.6)	9.3	(±3.3)
B	102.2	(± 5.3)	19.0	(± 4.1)	12.5	(±1.1)	1.85	(±0.3)
C	120.0	(± 5.4)	24.2	(± 4.5)	15.3	(±0.91)	2.20	(±0.18)
D	104.2	(± 5.4)	14.75	(± 3.2)	13.8	(±0.85)	1.48	(±0.25)
	Seed No.				Seed wgt. (kg)			
A	161.0	(±13.8)	143.5	(±13.5)	5.1	(±0.35)	5.8	(±0.5)
B	141.2	(±4.2)	81.2	(± 3.0)	4.8	(±0.08)	2.8	(±0.14)
C	143.3	(±8.7)	89.0	(± 9.5)	5.1	(±0.35)	2.8	(±0.31)
D	129.0	(±5.5)	71.5	(± 9.0)	4.2	(±0.26)	2.4	(±0.33)
	Total No.				Total wgt. (kg)			
A	280.0	(±20.2)	217.0	(±35.8)	19.3	(±1.6)	15.1	(±3.6)
B	243.0	(±21.6)	99.0	(± 8.4)	17.3	(±1.1)	4.6	(±0.50)
C	263.0	(±11.5)	111.0	(±11.5)	20.3	(±0.9)	5.0	(±0.69)
D	233.0	(±10.5)	86.3	(±11.4)	17.9	(±0.8)	3.9	(±0.56)
1981								
	Table No.				Table wgt. (kg)			
	5.3	(±2.2)	45.0	(±2.8)	4.9	(±0.4)	0.50	(±0.5)
	Seed No.				Seed wgt. (kg)			
	127.0	(±13.2)	100.0	(±2.6)	10.4	(±3.2)	3.6	(±1.8)
	Total No.				Total wgt. (kg)			
	172.0	(±13.2)	100.0	(±2.6)	10.4	(±3.2)	3.6	(±1.8)

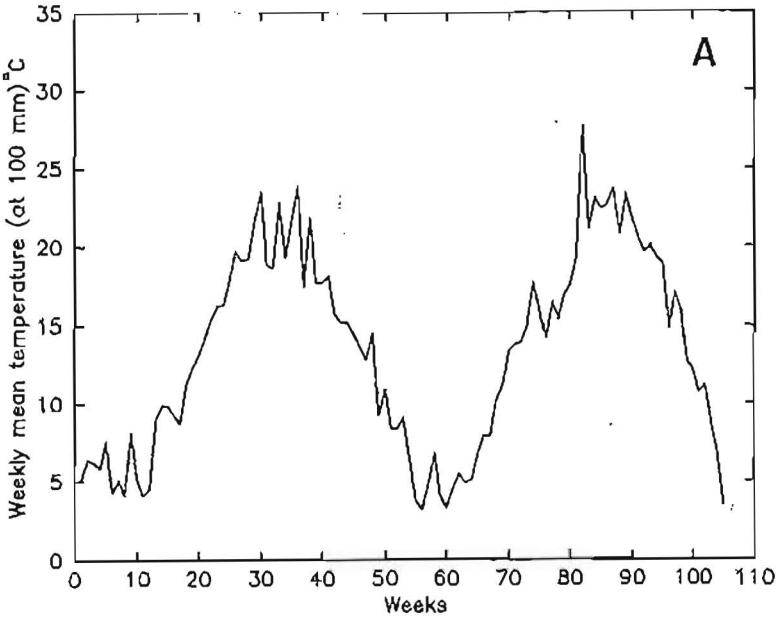
APPENDIX VII

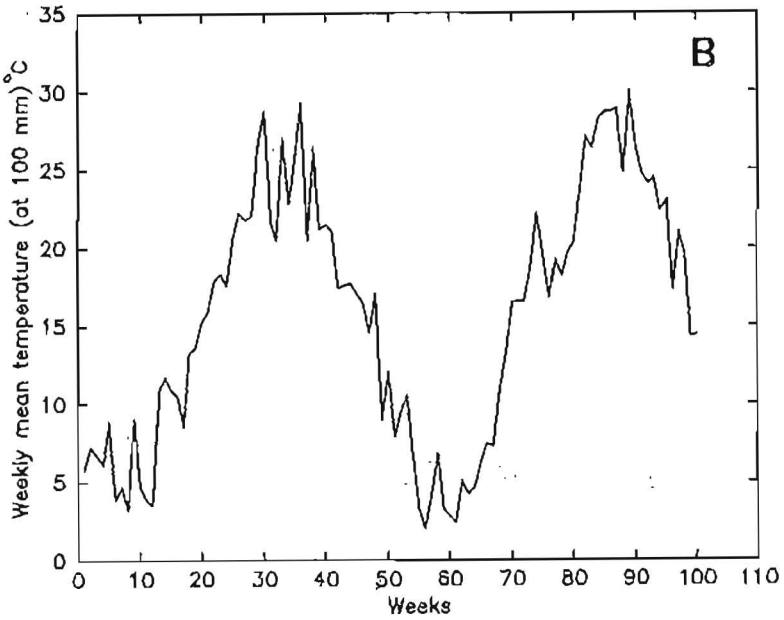
Mean weekly soil temperature (°C) at 100 mm depth at three sites over the two years that the study was carried out.

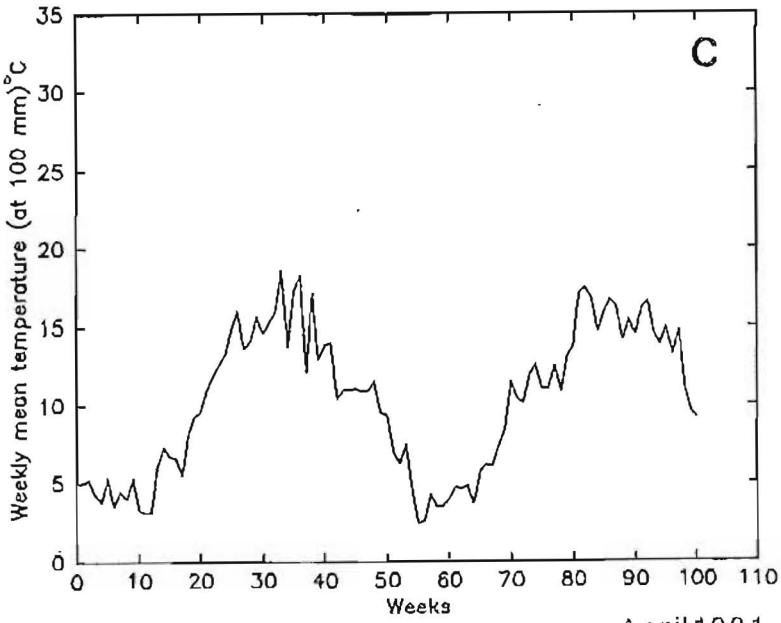
A = In silt at S4

B = In peat at Cranford St.

C = In silt loam at Outram.





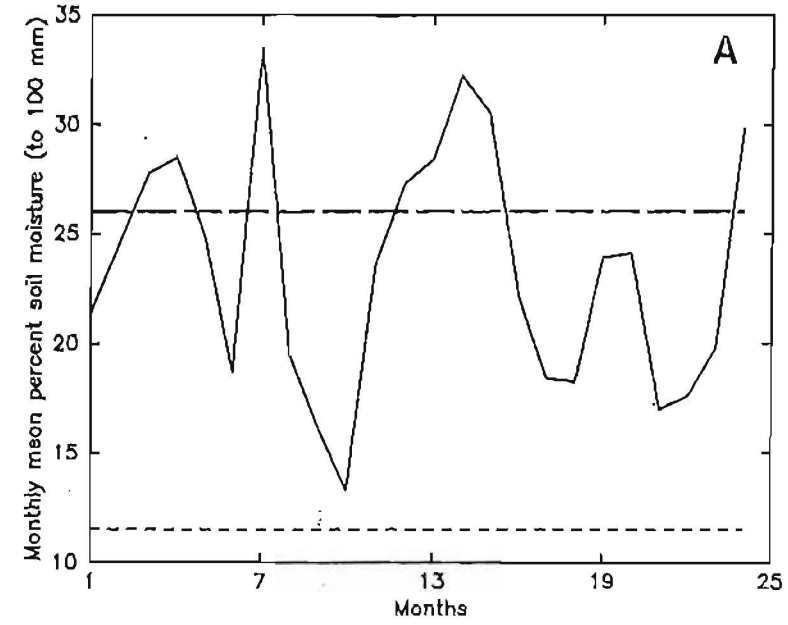


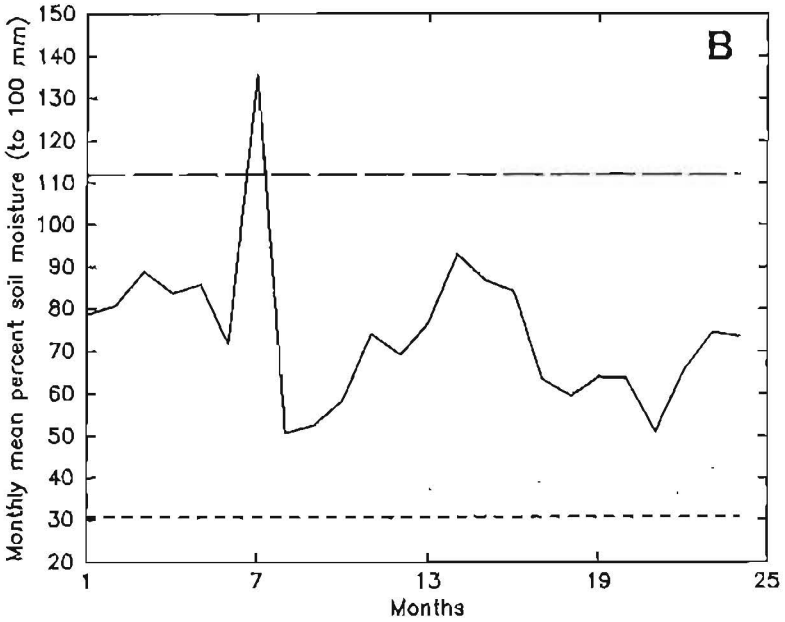
June 1979 April1981

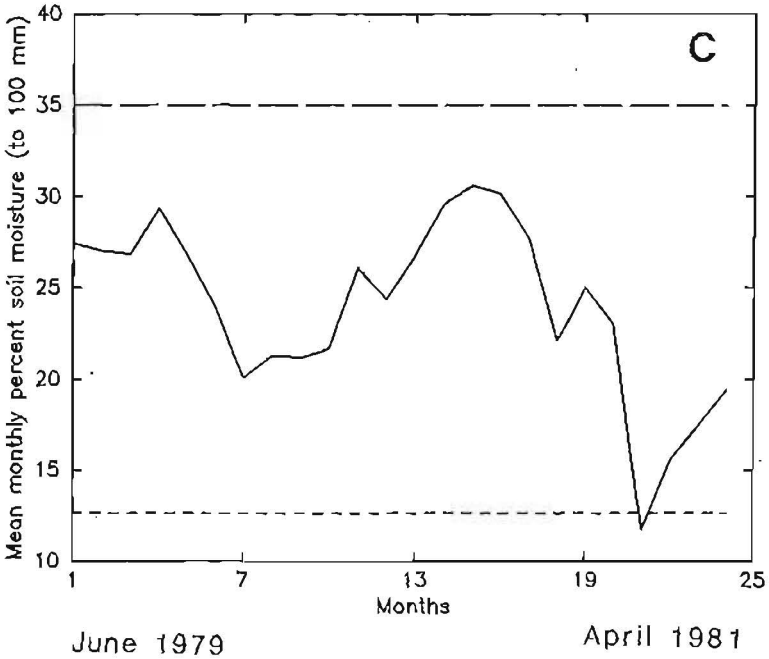
APPENDIX VIII

Mean monthly soil moisture (as percentage oven dry weight) at three sites over the two years that the study was being carred out.

A = in silt at S4
B = in peal at Cranford St.
C = in silt loam at Outram







June 1979 April 1981

APPENDIX IX

Detail of life styles present in a single generation of cyst nematode (after Foot, 1978b).

Life style A occurs within the cyst and involves the egg, first stage juvenile, and early life of the second stage juvenile. It is a resting stage particularly suited to survival in adverse conditions and in the absence of suitable hosts. However, in this study only the activated part of this life style was examined, that is the period when the cyst is under the influence of host roots.

Life style B encompasses the active migration of the second stage juvenile from its parent cyst through the soil in search of a host root. It is successfully completed on penetration of the root by the second stage juvenile.

Life style C is the main feeding phase in which the sedentary second and third stage juveniles tap the host's resources via the syncitium. Sex of the developing nematode is determined by size of induced syncitium and hence by food supply.

Life style D is the final phase, which terminates in reproduction. It includes fourth stage juveniles (sub-adults) and adults, both of which show sexual divergence in function and in survival hurdles: feeding continues in fourth stage larvae and adult females, both of which retain their sedentary state but become swollen and eventually protrude through the host root cortex; on the other hand, the fourth stage male does not feed and is merely an immobile transition stage between the sedentary feeding juvenile and the free-living, non-feeding vermiform adult whose sole function is to locate and fertilise young adult females. Since mating is essential to reproduction successful male function within life style D is implicit in the production of viable eggs by the adult female. Successful completion of this life style was therefore based on the survival of females to become mature cysts (entry phase 5, see Table 5.1). Suitable correction factors were used to retain cohort parity between this and the other four entry phases (Appendix XVI).

Appendix X: Data collected from the early planted cohort series of *O. pallida* at St Lincoln, presented as mean values with Standard Deviation and the number of replicates, parameters defined in Table 5.3.

t = days
n = sample No.

	13/3/80												
	t=0 n=8	t=6 n=1	t=13 n=2	t=16 n=3	t=20 n=4	t=28 n=5	t=34 n=6	t=35 n=7	t=39 n=8	t=42 n=9	t=45 n=10	t=49 n=11
S	104	-	-	-	-	-	-	-	-	-	-	-
Rinoc	247.2(29.5;8)	-	-	-	-	-	-	-	-	-	-	-
A	25768	-	-	-	-	-	-	-	-	-	-	-
bn	.180(.03;8)	.808(.05;6)	.816(.02;4)	.774(.01;4)	.786(.04;4)	.670(.03;3)	.629(.05;3)	.537(.03;3)	.344(.17;4)	.042(.02;4)	-	.033(.03;4)
vn	.033(.01;8)	.031(.01;4)	.030(.0;4)	.031(.01;4)	.032(.01;4)	.028(.01;4)	.033(.01;4)	.033(.01;3)	.041(.01;3)	.109(.02;3)	-	.076(.02;4)
dn	.187(.03;8)	.180(.01;4)	.153(.02;4)	.194(.01;4)	.381(.04;4)	.309(.06;4)	.272(.04;3)	.368(.07;4)	.413(.16;3)	.843(.03;3)	-	.868(.02;4)
f1n	-	-	-	-	184(38;4)	856(44;4)	616(91;4)	4249(6));4)	9305(816;4)	10025(999;4)	-	3590(384;4)
f2n	-	-	-	-	-	-	24(.5;4)	857(16;4)	856(91;4)	5712(416;4)	-	3285(88;4)
f3n	-	-	-	-	-	-	-	-	-	32(.41;4)	-	460(61;4)
Sea	-	-	-	-	-	-	-	-	-	0.0(0.0;4)	0.0(.01;3)	.03(.07;4)
In	-	-	-	-	-	-	-	-	-	-	-	388(48;4)
kn	-	-	-	-	-	-	-	-	-	-	-	-
bf1n	-	-	-	-	-	-	-	-	-	-	-	-
cf1n	-	-	-	-	-	-	-	-	-	-	-	-
df1n	-	-	-	-	-	-	-	-	-	-	-	-
Hin	-	-	-	-	-	-	-	-	-	-	-	-
ar tot	-	-	-	-	-	-	-	-	-	-	-	-
y	-	-	-	-	-	-	-	-	-	-	-	-
P	-	-	-	-	-	-	-	-	-	-	-	-
V.P.	-	-	-	-	-	-	-	-	-	-	-	-

	5/5/81										
t=46 n=12	t=49 n=13	t=53 n=14	t=60 n=15	t=67 n=16	t=81 n=17	t=101 n=18	t=116 n=19				
-	-	-	-	-	-	-	-	S			
-	-	-	-	-	-	-	-	Rinoc			
-	-	-	-	-	-	-	-	A			
.037(.06;4)	-	-	-	-	-	-	.025(0.44;4)	bn			
.131(.03;4)	-	-	-	-	-	-	.102(.01;4)	vn			
.841(.09;4)	-	-	-	-	-	-	.867(.02;4)	dn			
5740(684;4)	-	-	-	-	-	-	-	f1n			
5866(31;4)	-	2453(681;4)	-	-	-	-	-	f2n			
7838(303;4)	-	504(78;4)	-	-	-	-	-	f3n			
.59(.07;4)	-	-	.94(.05; 3	-	-	-	-	Sea			
3586(424;4)	-	4567(615;4)	5535(535;4)	-	-	-	5383(195;4)	In			
1.5(.23;4)	3.6(.3;4)	6.9(.50;4)	32.8(1.1;4)	56.6(2.6;4)	113.7(12.9;4)	217.3(41.8;4)	360(32;4)	kn			
-	-	-	-	-	-	-	.042(.04;4)	bf1n			
-	-	-	-	-	-	-	.103(.03;4)	cf1n			
-	-	-	-	-	-	-	.854(.05;4)	df1n			
-	-	-	-	-	-	-	5232	Hin			
-	-	-	-	-	-	-	.401	ar tot			
-	-	-	-	-	-	-	.940	V			
-	-	-	-	-	-	-	1,340,841	P			
-	-	-	-	-	-	-	1,279,192	V.P.			

Appendix A Data collected from the early plant cohort series of *G. rostochiensis* at St Lincoln, presented as means values Standard Deviation and the number of replicates, Parameters defined in Table 5.3.

t = days n = sample No.	13/11/80 t=0 n=0	t=4 n=1	t=7 n=2	t=11 n=3	t=14 n=4	t=18 n=5	t=21 n=6	t=25 n=7	t=28 n=8	t=32 n=9	t=35 n=10	t=39 n=11
S	151	-	-	-	-	-	-	-	-	-	-	-
Xinoc	187(10.6:8)	-	-	-	-	-	-	-	-	-	-	-
a	28351	-	-	-	-	-	-	-	-	-	-	-
bn	.689(.06:8)	.695(.02:4)	.690(.04:4)	.581(.04:4)	.518(.08:4)	.484(.07:4)	.392(.05:4)	.286(.04:4)	.170(.11:4)	.048(.03:5)	-	.077(.03:4)
cn	.084(.02:8)	.062(.02:4)	.043(.01:4)	.062(.01:4)	.055(.01:4)	.065(.03:4)	.061(.01:4)	.074(.01:4)	.093(.02:4)	.114(.03:4)	-	.115(.04:4)
dn	.254(.01:8)	.242(.01:4)	.264(.04:4)	.353(.04:4)	.426(.08:4)	.450(.06:4)	.545(.03:4)	.638(.03:4)	.735(.13:4)	.837(.02:4)	-	.766(.09:4)
f_{1n}	-	-	45(4.1:4)	56(3.1:4)	404(24:4)	648(81:4)	434(14:4)	3496(96:4)	7580(101:4)	4979(202:4)	-	1075(111:4)
f_{2n}	-	-	-	-	-	-	12(.46:4)	630(28:4)	1459(181:4)	4012(298:4)	-	1134(322:4)
f_{3n}	-	-	-	-	-	-	-	-	-	86(.69:4)	-	587(68:4)
s_{FR}	-	-	-	-	-	-	-	-	-	0.0(.01:4)	0.0(.01:4)	309(.04:4)
s_n	-	-	-	-	-	-	-	-	-	-	-	257.9(34.5:4)
k_n	-	-	-	-	-	-	-	-	-	-	-	-
bf_{1n}	-	-	-	-	-	-	-	-	-	-	-	-
cf_{1n}	-	-	-	-	-	-	-	-	-	-	-	-
df_{1n}	-	-	-	-	-	-	-	-	-	-	-	-
$1f_{1n}$	-	-	-	-	-	-	-	-	-	-	-	-
$ertot$	-	-	-	-	-	-	-	-	-	-	-	-
V	-	-	-	-	-	-	-	-	-	-	-	-
P	-	-	-	-	-	-	-	-	-	-	-	-
V.P.	-	-	-	-	-	-	-	-	-	-	-	-

t=46 n=12	t=49 n=13	t=53 n=14	t=60 n=15	t=67 n=16	t=81 n=17	t=104 n=18	8/3/81 t=116 n=19	
								S
								Xinoc
								a
.036(.04:4)	-	-	-	-	-	-	.031(.03:4)	bn
.142(.03:4)	-	-	-	-	-	-	.167(.03:4)	cn
.814(.07:4)	-	-	-	-	-	-	.806(.05:4)	dn
894(88:4)	-	-	-	-	-	-	-	f_{1n}
1946(190:4)	-	265(58:4)	-	-	-	-	-	f_{2n}
6748(300:4)	-	600(49:4)	318(96:4)	-	-	-	-	f_{3n}
.629(.17:4)	-	.936(.12:4)	-	-	-	-	-	s_{FR}
318.8(.93:4)	-	5917(393:4)	4177(515:4)	-	-	-	4420(513:4)	t_n
.80(.16:4)	3.1(.35:4)	4.4(.44:4)	49.9(53.4)	49.9(5.3:4)	122.5(29.7:4)	228.1(305:4)	290(40:4)	k_n
-	-	-	-	-	-	-	.049(.07:4)	bf_{1n}
-	-	-	-	-	-	-	355(.02:4)	cf_{1n}
-	-	-	-	-	-	-	.792(.01:4)	df_{1n}
-	-	-	-	-	-	-	4)71	$1f_{1n}$
-	-	-	-	-	-	-	.533	er_{tot}
-	-	-	-	-	-	-	.920	V
-	-	-	-	-	-	-	1,314,258	P
-	-	-	-	-	-	-	1,114,357	V.P.

Appendix XI Data collected from early planting cohorts series of *O. rosaceolensis* at Cranford St., presented as mean values with Standard Deviation and mean numbers, parameters defined in Table. 5.3.

t=days n=sample No.	t=0 n=0	t=4 n=1	t=7 n=2	t=11 n=3	t=14 n=4	t=18 n=5	t=21 n=6	t=25 n=7	t=28 n=8	t=32 n=9	t=35 n=10	t=39 n=11	t=46 n=12
S	151	-	-	-	-	-	-	-	-	-	-	-	-
X(max	189(20.6:8)	-	-	-	-	-	-	-	-	-	-	-	-
A	28,351	-	-	-	-	-	-	-	-	-	-	-	-
bn	.698(.06:4)	.648(.04:4)	.511(.08:4)	.491(.039:4)	.409(.04:4)	.206(.03:4)	.340(.08:4)	.174(.06:4)	.122(.14:4)	.064(.04:4)	.060(.04:4)	.056(.06:4)	.044(.03:4)
cn	.064(.03:4)	.054(.02:4)	.069(.01:4)	.053(.01:4)	.067(.03:4)	.078(.01:4)	.084(.01:4)	.094(.01:4)	.093(.03:4)	.151(.04:4)	.136(.02:4)	.139(.02:4)	.111(.04:4)
dn	.237(.01:4)	.261(.03:4)	.386(.07:1)	.436(.03:4)	.553(.06:4)	.716(.06:4)	.774(.10:4)	.751(.06:4)	.784(.11:4)	.803(.07:4)	.800(.06:4)	.804(.08:4)	.843(.01:4)
f_{1n}	-	-	18(1.6:4)	194(20:4)	478(36:4)	1834(303:4)	1703(354:4)	1930(206:4)	1018(301:4)	1058(222:4)	361(21:4)	23(1.6:4)	-
f_{2n}	-	-	-	-	16(13:4	406(26:4)	1664(616:4)	1623(388:4)	4060(291:4)	1473(681:4)	635(28:4)	163(38:4)	-
f_{3n}	-	-	-	-	-	-	170(17:4)	2870(248:4)	4653(368:4)	1503(360:4)	1543(341:4)	1309(346:4)	458(68:4)
Sen	-	-	-	-	-	-	-	.198(.06:4)	.371(.08:4)	.307(.14:4)	.357(.08:4)	.603(.06:4)	.593(.40:4)
fn	-	-	-	-	-	-	-	-	3513(1331:4)	1936(460:4)	4123(811:4)	5377(727:4)	4451(1201:4)
kn	-	-	-	-	-	-	-	-	-	-	5.3(.53:4)	26.8(1.4:4)	63.2(2.8:4)
bfin	-	-	-	-	-	-	-	-	-	-	-	-	-
cfin	-	-	-	-	-	-	-	-	-	-	-	-	-
dfin	-	-	-	-	-	-	-	-	-	-	-	-	-
ffin	-	-	-	-	-	-	-	-	-	-	-	-	-
error	-	-	-	-	-	-	-	-	-	-	-	-	-
Y	-	-	-	-	-	-	-	-	-	-	-	-	-
P	-	-	-	-	-	-	-	-	-	-	-	-	-
W.P.	-	-	-	-	-	-	-	-	-	-	-	-	-

t=53 n=13	t=60 n=13	t=67 n=14	t=81 n=13	t=104 n=16	9/3/81 t=116 n=17	t=days n=sample No.
-	-	-	-	-	-	S
-	-	-	-	-	-	Xlmax
-	-	-	-	-	-	A
-	-	-	-	-	.017(.01:4)	bn
-	-	-	-	-	.163(.03:4)	cn
-	-	-	-	-	.818(.02:4)	dn
-	-	-	-	-	-	f_{1n}
-	-	-	-	-	-	f_{2n}
-	-	-	-	-	-	f_{3n}
-	-	-	-	-	-	Sen
4436(798:4)	4833(798:4)	4431(722:4)	-	-	3030(349:4)	fn
84.7(11.7:4)	100.8(11.1:4)	85(11.1:4)	100(28:4)	215.8(42:4)	244.7(27:4)	kn
-	-	-	-	-	.103(.09:32)	bfin
-	-	-	-	-	.137(.03:16)	cfin
-	-	-	-	-	.783(.07:32)	dfin
-	-	-	-	-	4334	ffin
-	-	-	-	-	.367	error
-	-	-	-	-	0.85	Y
-	-	-	-	-	325,536	P
-	-	-	-	-	299,748	W.P.

Appendix XI Data collected from early planted cohorts series of *C. pallida* at Cranford St, presented as mean values with Standard Deviation and number of replicates, parameters defined in Table 3.3.

t=days n=sample No.	13/11/80 t=0 n=0	t=4 n=3	t=5 n=9	t=11 n=3	t=14 n=4	t=18 n=5	t=21 n=8	t=25 n=7	t=28 n=8	t=32 n=9	t=35 n=10	t=39 n=11	t=46 n=12
R	104	-	-	-	-	-	-	-	-	-	-	-	-
Kinoc	243(29:8)	-	-	-	-	-	-	-	-	-	-	-	-
A	33766	-	-	-	-	-	-	-	-	-	-	-	-
bn	.780(.03:8)	.787(.03:4)	.756(.05:4)	.640(.071:4)	.672(.02:4)	.531(.11:4)	.264(.08:4)	.269(.13:4)	.040(.02:4)	.036(.03:4)	.041(.03:4)	.043(.02:4)	.031(.01:4)
cn	.033(.01:8)	.026(.01:4)	.028(.01:4)	.030(.05:4)	.031(.05:4)	.039(.01:4)	.029(.01:4)	.036(.01:4)	.044(.01:4)	.083(.02:4)	.090(.02:4)	.089(.01:4)	.101(.03:4)
dn	.187(.03:8)	.186(.03:4)	.213(.03:4)	.328(.07:4)	.298(.03:4)	.429(.09:4)	.706(.09:4)	.694(.13:4)	.914(.01:4)	.879(.04:4)	.869(.04:4)	.867(.02:4)	.867(.05:4)
f_{1n}	-	-	-	248(72:4)	382(68:4)	2658(304:4)	1753(242:4)	1760(368:4)	1639(261:4)	1545(196:4)	792(64:4)	136(61:4)	-
f_{2n}	-	-	-	-	18(24:4)	188(16:4)	428(19:4)	1984(388:4)	3301(368:4)	2859(145:4)	3448(404:4)	827(360:4)	-
f_{3n}	-	-	-	-	-	-	-	774(36:4)	3006(247:4)	3338(368:4)	3585(368:4)	3712(685:4)	572(68:4)
Brn	-	-	-	-	-	-	-	-	.186(.02:4)	.206(.09:4)	.314(.06:4)	.466(.11:4)	.333(.12:4)
in	-	-	-	-	-	-	-	-	1227(591:4)	2613(508:4)	2761(365:4)	3688(661:4)	3355(284:4)
kn	-	-	-	-	-	-	-	-	-	-	3.3(.6:4)	16.3(1.3:4)	47.2(4.6:4)
bfin	-	-	-	-	-	-	-	-	-	-	-	-	-
cfin	-	-	-	-	-	-	-	-	-	-	-	-	-
dfin	-	-	-	-	-	-	-	-	-	-	-	-	-
Ifin	-	-	-	-	-	-	-	-	-	-	-	-	-
srtot	-	-	-	-	-	-	-	-	-	-	-	-	-
V	-	-	-	-	-	-	-	-	-	-	-	-	-
P	-	-	-	-	-	-	-	-	-	-	-	-	-
V.P.	-	-	-	-	-	-	-	-	-	-	-	-	-

t=53 n=13	t=60 n=11	t=67 n=15	t=81 n=16	t=104 n=17	9/3/81 t=136 n=18	t=days n=sample No.
-	-	-	-	-	-	R
-	-	-	-	-	-	Kinoc
-	-	-	-	-	-	A
-	-	-	-	-	.021(.01:4)	bn
-	-	-	-	-	.102(.01:4)	cn
-	-	-	-	-	.876(.02:4)	dn
-	-	-	-	-	-	f_{1n}
-	-	-	-	-	-	f_{2n}
-	-	-	-	-	-	f_{3n}
-	-	-	-	-	-	Brn
3301(265:4)	3378(362:4)	3168(321:4)	3509(467:4)	-	3560(628:4)	in
85.3(15.3:4)	73.0(7.0:4)	80.3(3.4:4)	176(32.4:4)	88.6(8.1:4)	207.3(30.9:4)	kn
-	-	-	-	-	.054(.03:20)	bfin
-	-	-	-	-	.094(.02:16)	cfin
-	-	-	-	-	.881(.05:20)	dfin
-	-	-	-	-	3383	Ifin
-	-	-	-	-	.302	srtot
-	-	-	-	-	0.44	V
-	-	-	-	-	702,967	P
-	-	-	-	-	61,678	V.P.

ndix XII Data collected from late planted cohort series of *C. rostochiensis* at S_4 Lincoln, presented as mean values with Standard Deviation and number of replicates, parameters defined in Table 5.3.

t=days n=sample No.	t=0 n=0	t=4 n=1	t=7 n=2	t=10 n=3	t=14 n=4	t=17 n=5	t=21 n=6	t=24 n=7	t=28 n=8	t=35 n=9	t=46 n=10	t=53 n=11	t=64 n=12	t=69 n=13	t=76 n=14	t=days n=sample No.
S	151	–	–	–	–	–	–	–	–	–	–	–	–	–	–	S
Kinoc	189(10.6:8)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	Kinoc
a	28551	–	–	–	–	–	–	–	–	–	–	–	–	–	–	a
bn	.698(.06:8)	.668(.01:4)	.707(.02:4)	.519(.11:4)	.184(.06:4)	.098(.04:4)	.079(.01:4)	.026(.02:4)	.017(.01:4)	–	–	–	–	–	.026(.01:4)	bn
cn	.064(.02:8)	.089(.01:4)	.072(.03:4)	.097(.02:4)	.070(.03:4)	.115(.02:4)	.117(.02:4)	.060(.01:4)	.070(.02:4)	–	–	–	–	–	.091(.24:4)	cn
dn	.237(.01:8)	.242(.02:4)	.219(.03:4)	.383(.12:4)	.745(.08:4)	.785(.06:4)	.803(.04:4)	.913(.03:4)	.912(.01:4)	–	–	–	–	–	.881(.02:4)	dn
f_{1n}	–	–	–	21(10:4)	649(38:4)	1552(164:4)	2210(184:4)	832(64:4)	413(28:4)	28(32:4)	–	–	–	–	–	f_{1n}
f_{2n}	–	–	–	–	155(26:4)	284(28:4)	2310(207:4)	5698(368:4)	4600(447:4)	155(36:4)	–	–	–	–	–	f_{2n}
f_{3n}	–	–	–	–	–	–	472(36:4)	1411(400:4)	5609(381:4)	1571(447:4)	401(36:4)	–	–	–	–	f_{3n}
Srn	–	–	–	–	–	–	.048(.057:4)	.381(.09:4)	.421(.11:4)	.821(.06:4)	.806(.05:4)	–	–	–	–	Srn
in	–	–	–	–	–	–	–	1753(300:4)	2642(204:4)	3203(299:4)	3498(446:4)	–	–	–	2455(802:4)	in
kn	–	–	–	–	–	–	–	–	–	35.9(1.9:4)	35.5(2.2:4)	43.9(0.9:4)	93.2(4.9:4)	142(3.9:4)	185(62.4:4)	kn
bfin	–	–	–	–	–	–	–	–	–	–	–	–	–	–	.050(.04:20)	bfin
cfin	–	–	–	–	–	–	–	–	–	–	–	–	–	–	.087(.02:36)	cfin
dfin	–	–	–	–	–	–	–	–	–	–	–	–	–	–	.902(0.27:12)	dfin
ifin	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3126	ifin
srtot	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.472	srtot
V	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.91	V
P	–	–	–	–	–	–	–	–	–	–	–	–	–	–	579,837	P
V.P.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	527,684	V.P.

Appendix XII Data collected from late planted cohort series of *G. pallida* at S_4 Lincoln, presented as mean values with Standard Deviation and number of replicates, parameters defined in Table 5.3.

t=days n=sample No.	21/12/80 t=0 n=0	t=4 n=1	t=7 n=2	t=10 n=3	t=14 n=4	t=17 n=5	t=21 n=6	t=24 n=7	t=28 n=8	t=35 n=9	t=46 n=10	t=53 n=11	t=64 n=12	t=69 n=13	9/3/81 t=76 n=14	t=days n=sample No.
S	104	-	-	-	-	-	-	-	-	-	-	-	-	-	-	S
Kinoc	247(29.5:8)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	Kinoc
a	25766	-	-	-	-	-	-	-	-	-	-	-	-	-	-	a
bn	.780(.03:8)	.801(.03:4)	.80(.03:4)	.784(.03:4)	.447(.04:4)	.334(.06:4)	.173(.03:4)	.102(.01:4)	.072(.02:4)	-	-	-	-	-	.068(.01:4)	bn
cn	.033(01:8)	.063(.01:4)	.071(.01:4)	.069(.01:4)	.052(.02:4)	.034(02:4)	.069(.18:4)	.061(.01:4)	.068(.02:4)	-	-	-	-	-	.062(.01:4)	cn
dn	.187(.03:8)	.126(.02:4)	.127(.03:4)	.146(.03:4)	.500(.02:4)	.630(06:4)	.757(.04:2)	.835(.01:4)	.858(.03:4)	-	-	-	-	-	.869(.02:4)	dn
f_{1n}	-	-	-	-	970(88:4)	518(75:4)	1613(304:4)	433(100:4)	9(10:4)	2(.1:4)	-	-	-	-	-	f_{1n}
f_{2n}	-	-	-	-	125(18:4)	80(45:4)	1833(168:4)	2084(200:4)	950(98:4)	3(.01:4)	-	-	-	-	-	f_{2n}
f_{3n}	-	-	-	-	-	-	576(36:4)	1341(200:4)	1090(100:4)	7(.6:4)	160(84:4)	-	-	-	-	f_{3n}
Srn	-	-	-	-	-	-	.121(.10:4)	.352(.02:4)	.505(.06:4)	.866(.16:4)	.562(.42:4)	-	-	-	-	Srn
in	-	-	-	-	-	-	-	812(112:4)	929(98.9:4)	1687(127:4)	4111(328:4)	-	-	-	2445(646:4)	in
kn	-	-	-	-	-	-	-	-	-	18.4(1.6:4)	42.2(2.7:4)	44.2(1.3:4)	109(9.2:4)	156(4.5:4)	197(27:4)	kn
bfin	-	-	-	-	-	-	-	-	-	-	-	-	-	-	.081(.02:12)	bfin
cfin	-	-	-	-	-	-	-	-	-	-	-	-	-	-	.062(.03:36)	cfin
dfin	-	-	-	-	-	-	-	-	-	-	-	-	-	-	.855(.03:12)	dfin
ifin	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1981	ifin
arcot	-	-	-	-	-	-	-	-	-	-	-	-	-	-	.378	arcot
V	-	-	-	-	-	-	-	-	-	-	-	-	-	-	.88	V
P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	392,039	P
V.P.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	344,995	V.P.

Appendix XIII Data collected from dune planted cohort series of *C. rostellariaefa* at Cronford St., presented as mean values with Standard Deviation and number of replicates. Parameters defined in Table 3.3.

t=days n=sample No.	21/13/80 t=0 n=0	t=4 n=1	t=7 n=2	t=10 n=3	t=14 n=4	t=17 n=5	t=21 t=6	t=24 n=7	t=28 n=8	t=31 n=9	t=35 n=10	t=39 n=11	t=42 n=12
$\bar{s}$	131	-	-	-	-	-	-	-	-	-	-	-	-
Xinoc	189(10.8:8)	-	-	-	-	-	-	-	-	-	-	-	-
s	28,551	-	-	-	-	-	-	-	-	-	-	-	-
bn	.698(06:8)	.767(.03:4)	.786(.034:4)	.770(.03:4)	.657(.03:4)	.501(.05:4)	.457(.13:4)	.234(.07:4)	.149(.07:4)	.057(.02:4)	.052(.02:4)	.04(.01:4)	-
cn	.044(021:8)	.046(.01:4)	.034(.01:4)	.058(.02:4)	.045(.01:4)	.054(.01:4)	.044(.01:4)	.048(.01:4)	.039(.01:4)	.038(.01:4)	.051(.01:4)	.035(.02:4)	-
dn	.232(01:8)	.183(.03:4)	.179(.03:4)	.171(.04:4)	.296(.06:4)	.443(.04:4)	.478(.15:4)	.713(.08:4)	.814(.08:4)	.903(.02:4)	.896(.03:4)	.896(.07:4)	-
f_{1n}	-	-	-	-	-	.336(13:4)	834(28:4)	932(36:4)	1445(368:4)	1179(491:4)	-	-	-
f_{2n}	-	-	-	-	-	-	-	659(38:4)	1347(304:4)	2182(360:4)	302(64:4)	-	-
f_{3n}	-	-	-	-	-	-	-	47(1.0:4)	0	1328(94:4)	3806(184:4)	478(36:4)	-
$\bar{s}_{rn}$	-	-	-	-	-	-	-	-	-	.239(.07:4)	.726(.05:4)	.631(.05:4)	-
f_{in}	-	-	-	-	-	-	-	-	-	353(98:4)	2438(181:4)	1748(583:4)	-
k_n	-	-	-	-	-	-	-	-	-	-	-	-	6.9(1.1:4)
bfin	-	-	-	-	-	-	-	-	-	-	-	-	-
cfin	-	-	-	-	-	-	-	-	-	-	-	-	-
dfin	-	-	-	-	-	-	-	-	-	-	-	-	-
ffin	-	-	-	-	-	-	-	-	-	-	-	-	-
artot	-	-	-	-	-	-	-	-	-	-	-	-	-
v	-	-	-	-	-	-	-	-	-	-	-	-	-
P	-	-	-	-	-	-	-	-	-	-	-	-	-
V.P.	-	-	-	-	-	-	-	-	-	-	-	-	-

t=46 n=13	t=49 n=14	t=53 n=15	t=61 n=16	9/3/81 t=76 n=17	n=sample t=days
-	-	-	-	-	$\bar{s}$
-	-	-	-	-	Xinoc
-	-	-	-	-	s
-	-	-	-	.040(.01:4)	bn
-	-	-	-	.055(.01:4)	cn
-	-	-	-	.903(.03:4)	dn
-	-	-	-	-	f_{1n}
-	-	-	-	-	f_{2n}
-	-	-	-	-	f_{3n}
-	-	-	-	-	$\bar{s}_{rn}$
-	-	-	-	3962(333:4)	f_{in}
21.3(9.6:4)	33.(6.4:4)	65.3(15.3:4)	169.3(15.5:4)	159.7(23.6:4)	k_n
-	-	-	-	.050(.02:4)	bfin
-	-	-	-	.049(.01:4)	cfin
-	-	-	-	.900(.03:4)	dfin
-	-	-	-	2048(468:4)	ffin
-	-	-	-	.544	artot
-	-	-	-	.93	v
-	-	-	-	323,836	P
-	-	-	-	299,749	V.P.

Appendix XIII Data collected from late planted cohort-region of *O. pallida* at Cranford St., presented as mean values with Standard Deviation and number of replicates, parameters defined in Table 3.3.

t=days n=sample No.	21/12/80 t=0 n=0	t=4 n=1	t=7 n=2	t=11 n=3	t=14 n=4	t=17 n=5	t=21 n=6	t=24 n=7	t=28 n=8	t=32 n=9	t=35 n=10	t=42 n=11	t=63 n=12
X	104	-	-	-	-	-	-	-	-	-	-	-	-
Xinoc	247(39.5±6)	-	-	-	-	-	-	-	-	-	-	-	-
A	35,776	-	-	-	-	-	-	-	-	-	-	-	-
bh	.720(.03±6)	.783(.03±4)	.771(.03±4)	.777(.01±4)	.803(.01±4)	.679(-.08)4)	.101(.15±4)	.333(.04±4)	.337(.09±4)	.063(.004±4)	.043(.01±4)	.045(.01±4)	-
ch	.033(.01±8)	.034(.01±4)	.041(.01±4)	.040(.01±4)	.040(.01±4)	.03±(.006±4)	.051(.01±4)	.035(.01±4)	.034(.02±4)	.047(.01±4)	.039(.01±4)	.048(.01±4)	-
dh	.187(.05±8)	.179(.02±4)	.187(.03±4)	.182(.01±4)	.182(.01±4)	.285(.09±4)	.366(.16±4)	.630(.04±4)	.707(.104±4)	.887(.03±4)	.913(.01±4)	.904(.01±4)	-
f1h	-	-	-	-	-	114(24±4)	424(36±4)	971(51±4)	1758(58±4)	810(54±4)	100(84±4)	28(1.4±4)	-
f2h	-	-	-	-	-	-	-	101(28±4)	547(100±4)	3761(300±4)	17358(309±4)	33527(26)±4)	-
f3h	-	-	-	-	-	-	-	-	84(18±4)	2004(384±4)	8743(223±4)	21028(300±4)	51.(18±4)
Sxh	-	-	-	-	-	-	-	-	-	.102(.06±4)	.47(.08±4)	.41(08±4)	-
fn	-	-	-	-	-	-	-	-	-	190.3(36±4)	287(48±4)	1475(350±4)	-
kn	-	-	-	-	-	-	-	-	-	-	-	-	6.5(.01±4)
bfin	-	-	-	-	-	-	-	-	-	-	-	-	-
cfin	-	-	-	-	-	-	-	-	-	-	-	-	-
dfin	-	-	-	-	-	-	-	-	-	-	-	-	-
ffin	-	-	-	-	-	-	-	-	-	-	-	-	-
errtot	-	-	-	-	-	-	-	-	-	-	-	-	-
V	-	-	-	-	-	-	-	-	-	-	-	-	-
F	-	-	-	-	-	-	-	-	-	-	-	-	-
V.F.	-	-	-	-	-	-	-	-	-	-	-	-	-

t=46 n=13	t=49 n=14	t=53 n=15	t=64 n=16	9/3/81 t=76 n=17	t=days n=sample No.
-	-	-	-	-	g
-	-	-	-	-	Xinoc
-	-	-	-	-	A
-	-	-	-	.046(.01±4)	bh
-	-	-	-	.043(.01±4)	ch
-	-	-	-	.906(.01±4)	dh
-	-	-	-	-	f1h
-	-	-	-	-	f2h
-	-	-	-	-	f3h
-	-	-	-	-	Sxh
-	-	-	-	1323(389±4)	fn
35.3(1.0±4)	36.3(.09±4)	39.2(.06±4)	173.3(6.0±4)	134.0(22.8±4)	kn
-	-	-	-	.031(-.02±4)	bfin
-	-	-	-	.041(.03±4)	cfin
-	-	-	-	.904(.01±4)	dfin
-	-	-	-	1400(371±4)	ffin
-	-	-	-	.331	errtot
-	-	-	-	.93	V
-	-	-	-	187,800	F
-	-	-	-	174,663	V.F.

XIV

Appendix. Data collected from early harvesting cohort series of *S. mansoni* at Butawa, presented as mean values with Standard Deviations and mean values, parameters defined in Table 5.3.

t=day	15/6/79													23/11/79
n=sample No.	t=0 n=0	t=19 n=1	t=26 n=2	t=33 n=3	t=40 n=4	t=48 n=5	t=61 n=6	t=69 n=7	t=75 n=8	t=82 n=9	t=89 n=10	t=98 n=11	t=100 n=12
$\bar{x}$	224	-	-	-	-	-	-	-	-	-	-	-	-
$\bar{x}_{inoc}$	108.4(15.4:8)	-	-	-	-	-	-	-	-	-	-	-	-
$\bar{x}$	24246	-	-	-	-	-	-	-	-	-	-	-	-
k_n	.346(.09:10)	.102(.02:4)	.080(.01:4)	.052(.06:4)	.042(.06:4)	.048(06:4)	-	-	-	-	-	-	.060(.03:10)
c_n	.037(06:10)	.063(.02:4)	.050(.03:4)	.064(.04:4)	.063(.01:4)	.068(04:4)	-	-	-	-	-	-	.034(.02:4)
d_n	.357(.06:10)	.655(.03:4)	.860(.03):4)	.891(.04:4)	.893(.01:4)	.875(.01:4)	-	-	-	-	-	-	.866(.03:10)
f_{1n}	-	243(12:4)	357(36:4)	368(2):4)	913(32:4)	691(8:4)	836(82:4)	164(28:4)	-	-	-	-	-
f_{2n}	-	-	-	-	48(6:4)	176(31:4)	809(32:4)	1881(160:4)	1367(364:4)	341(166:4)	161(84:4)	206(72:4)	6(18:4)
f_{3n}	-	-	-	-	-	-	600(65:4)	3793(301:4)	4449(389:4)	3076(606:4)	3455(301:4)	1334(204:4)	64(61:4)
Σ_{fn}	-	-	-	-	-	-	.0491(.06:4)	.2981(.02:4)	.3981(.13:4)	.4886(.09:4)	.4956(.09:4)	.4356(.05:4)	.4099(.06:4)
l_n	-	-	-	-	-	-	-	298.4(76.6:4)	263(022:4)	223(96:4)	440(36:4)	447(9):4)	340(13:4)
k_n	-	-	-	-	-	-	-	-	-	-	22.7(6.8:4)	21.7(5.2:4)	14.1(3.6:4)
b_{fin}	-	-	-	-	-	-	-	-	-	-	-	-	.038(.04:4)
c_{fin}	-	-	-	-	-	-	-	-	-	-	-	-	.067(.06:4)
d_{fin}	-	-	-	-	-	-	-	-	-	-	-	-	.873(02:4)
f_{fin}	-	-	-	-	-	-	-	-	-	-	-	-	410
$\bar{x}_{tot}$	-	-	-	-	-	-	-	-	-	-	-	-	0.408
$\bar{y}$	-	-	-	-	-	-	-	-	-	-	-	-	0.55
$\bar{\theta}$	-	-	-	-	-	-	-	-	-	-	-	-	16,331
V_n	-	-	-	-	-	-	-	-	-	-	-	-	9,368

t=(-5 n=13)	t=(11 n=14	t=118 n=15	t=128 n=16	8/1/80 t=118 n=17	t=days n=sample No.
-	-	-	-	-	$\bar{x}$
-	-	-	-	-	$\bar{x}_{inoc}$
-	-	-	-	-	$\bar{x}$
-	-	-	-	.033(.0:4)	k_n
-	-	-	-	.073(.0:4)	c_n
-	-	-	-	.894(01:4)	d_n
-	-	-	-	-	f_{1n}
38.4(9.1:4)	-	-	-	-	f_{2n}
426(28:4)	134(58:4)	107(36:4)	94(28:4)	-	f_{3n}
061(.04:4)	.146(.14:4)	.461(.24:4)	.137(.30:4)	-	Σ_{fn}
.284(.04:4)	514(3):4)	573(108:4)	493(118:4)	549(13):4)	l_n
96.(26:4)	106(38:4)	90.3(61:4)	116.)(36:4)	138.8(24:4)	k_n
-	-	-	-	.052(02:4)	b_{fin}
-	-	-	-	.087(03:4)	c_{fin}
-	-	-	-	.897(.03:4)	d_{fin}
-	-	-	-	532(103:16)	f_{fin}
-	-	-	-	.395	$\bar{x}_{tot}$
-	-	-	-	0.65	$\bar{y}$
-	-	-	-	84,481	$\bar{\theta}$
-	-	-	-	31,539	V_n

APPENDIX XV

Equations used in the construction of life tables (from Foot, 1978b).

The parameters measured during census of a cohort series were combined to produce the formulae listed in Appendix XVI for estimating the number of individuals surviving to each of the five entry phases (Table 5.1) of the potato cyst nematode life cycle. The formulae were derived as follows:

Entry phase 1: Effective eggs in initial cohort - This was the total number of live eggs at cohort initiation, ab_o, minus eggs still alive at the end of the series which were not stimulated to hatch by the host, $ab_{fin.}$, minus those eggs dying during the series which, if they had not died, would not have been stimulated to hatch.

$a.\overline{b}_{fin.}\ (c_{fin}-c_o)$, ($\overline{b}_{fin.}$ used to define the revelant proportion, $\overline{b}/\overline{b_o}$ thus assuming no difference in egg mortality between those able and those unable to be stimulated during the interval n = o to fin.).

That is: $$ab_o - ab_{fin.} - \frac{a.\ \overline{b}_{fin.}(c_{fin} - c_o)}{\overline{b_o}}$$

$$= \frac{a\,[b_o - b_{fin.}(1 + c_{fin.} - c_o)]}{b_o}$$

Entry phase 2: Number of second stage juveniles entering the soil - This was equal to the number of hatched eggs at final census, $ad_{fin.}$ minus the number of hatched eggs at cohort initiation, ad_o; that is $a(d_{fin}-d_o)$. Mortality of hatched second stage juveniles within the cyst was thus included in life style B rather than life style A.

Entry phases 3 & 4: Number of second stage juveniles penetrating the root system; and number of juveniles entering sub-adulthood - Measurements of parameters based on inoculum cyst status were of a cumulative nature, therefore allowing simple calculation of entry phases 1, 2 and 5. Measurements of within-root parameters (fl,

APPENDIX XVI

Formulae estimating of numbers surviving to each life style entry phase (after Foot, 1978b).

1. Effective eggs in initial cohort:

$$\frac{a[l_o - b_{fin.}(1 + c_{fin.} - c_o)]}{b_o}$$

2. Number of second stage juveniles entering soil:

$$a(d_{fin.} - d_o)$$

3. Number of second stage juveniles penetrating root system (Manly estimate):

$A_1 \theta/(1 - w_1)$ where A_1 is the area under the frequency curve of penetrated second stage juveniles,
θ is the survival parameter, and
w_1 is the stage specific survival rate

4. Number of juveniles entering sub-adulthood (Manly estimate):

$w_2[A_1\theta/(1 - w_1)]$ where w_2 is the survival rate in life style C (feeding juveniles).

5. Final number of breeding adults:

$$\frac{l_{fin.}(1 + sr_{tot.})}{1 - sr_{tot.}}$$

APPENDIX XVII

Key factors in population multiplication. The method of Varley and Gradwell (1960) was used where separate sub-mortalities for each life style were calculated as k-values (k=the key factor because it is the key to changes in population densities (Podolar and Rogers, 1975).

K values were calculated following Podolar and Rogers (1975) as:

$$k\text{-value} = \log_{10} N - \log_{10} N_s$$

and $$k = k_1 + K_2 + k_3 + \ldots k_n.$$

where N = the number of individuals before mortality,

N_s = the number surviving the mortality

K = the total generation mortality comprising the sum of a series of sub-mortalities. In this case

$$K = k_A + k_B + k_C + k_D$$

Graphical presentation of the results were shown in Figure 5.11.

K_A = life style A
K_B = life style B
K_C = life style C
K_D = life style D